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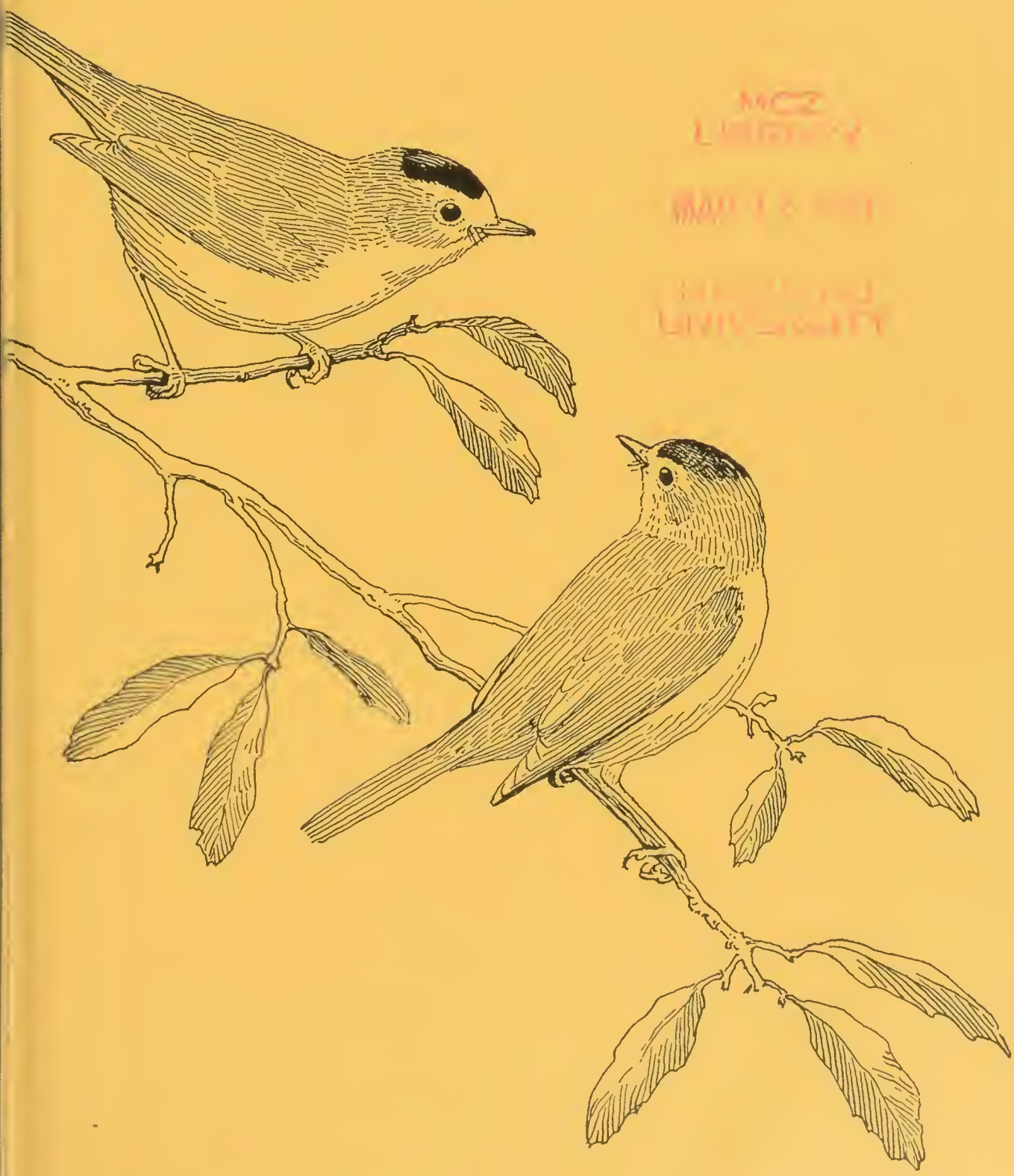

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The "black-capped" species-group of *Tangara* (females above, males below). *T. heinei,* upper left, range = stippled. *T. viridicollis, fulvigula* (male only), center left, and *T. v. viridicollis,* lower left, ranges = lines slanting downward to right (also present in the Cerros del Sira). *T. phillipsi*, sp. nov., center right, Cerros del Sira = star. *T. argyrofenges caeruleigularis*, lower right, range = lines slanting downward to left. Bolivian populations *(t. a. argyrofenges)* are similar to *T. a. caeruleigularis.* Acrylic and ink painting by Morton L. Isler.

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TANGARA PHILLIPSI, A NEW SPECIES OF TANAGER FROM THE CERROS DEL SIRA, EASTERN PERU

GARY R. GRAVES AND JOHN S. WESKE[1]

ABSTRACT.—A new species of tanager, *Tangara phillipsi* sp. nov., from the Cerros del Sira, Peru is described. *T. phillipsi* belongs to a monophyletic "black-capped" species complex of the Andean forest of western South America. *Received 29 Nov. 1985, accepted 21 Mar. 1986.*

Between 1969 and 1972, John Terborgh and Weske made collections in the previously unexplored Cerros del Sira, a series of isolated peaks (to 2450 m elevation) connected by a low-elevation ridge to the Eastern Cordillera of the Andes, which lies about 100 km to the west. Preliminary descriptions of the region and analyses of the ecology of the avifauna have been reported elsewhere (Weske and Terborgh 1971, 1977; Terborgh and Weske 1975). The evolutionary relationships of the avifauna of the Cerros del Sira and other Andean outliers to those of the Eastern Cordillera are of great interest. Here we report the discovery of a spectacular new species of tanager endemic to the Sira, related to *Tangara heinei* (Black-capped Tanager) and the "black-capped" species group of *Tangara* species (see Frontispiece).

Tangara phillipsi sp. nov.

SIRA TANAGER

HOLOTYPE.—American Museum of Natural History (AMNH) No. 820969; adult male from the Cerros del Sira 9°26′S, 74°45′W, 1300 m, Departamento de Huánuco, Peru, collected 26 July 1969, by John S. Weske; original number 2091.

DIAGNOSIS.—A medium-sized, sexually dichromatic *Tangara* most similar to *T. heinei*. The male differs from *T. heinei* in having the belly, breast, and sides of the neck (connecting

[1] Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

the crown and breast) black, instead of grayish-blue or blue (see Frontispiece). The contrasting throat patch is more restricted, and the tips of throat feathers are less bifurcated, and less elongated and pointed than in *T. heinei*. *T. phillipsi* is distinguished from *T. viridicollis* and *T. argyrofenges* in having grayish-blue edgings on wings and tail in conjunction with a metallic bluish-green throat patch as opposed to grayish-blue wings and yellowish-orange throat in *T. viridicollis* or black wings and tail and bluish-green throat in *T. argyrofenges*. Females differ from *T. heinei* by having a darker gray breast and belly, and less bifurcated, pointed throat feathers; from *T. viridicollis* in lacking a golden-olivaceous suffusion on crown, auriculars, and throat; and from *T. argyrofenges* in lacking bright yellowish-green flanks and back.

DESCRIPTION OF HOLOTYPE.—Eyering, lores, forehead, crown, and nape are glossy black, contrasting sharply with the back. The back, rump, upper tail coverts, sides of breast, and flanks silvery opalescent blue, the exact color varying with angle of reflected light. Remiges and upper wing coverts black; edges of the proximal ⅔–¾ of the outer web of primaries, except the outermost one; and the entire outer web of secondaries Slate-blue (capitalized color name is from Ridgway 1912). Inner webs of the secondaries edged with white. Several upper tail coverts, rump feathers, and wing coverts tinted with green, a character of predefinitive plumages in *T. heinei*, *T. argyrofenges*, and *T. viridicollis*. Underwing coverts white. Central pair of rectrices black along the shaft, the rest of the feather dull grayish-blue. The outermost pair of rectrices black: remaining rectrices black, edged with grayish-blue along the outer web. The throat patch appears bluish-green; feathers of the throat patch, which extends from just below the eyering and auriculars across the sides of the throat to extreme upper breast, black with glossy, metallic bluish-green tips. The posterior margin of the throat patch poorly defined with several glossy bluish-green feathers scattered among glossy black feathers of the upper breast. Lower breast and belly black, becoming slightly duller posteriorly, and bordered laterally by the opalescent blue sides of the breast and flanks. Tibial feathers white. Undertail coverts bluish-gray, faintly edged with white. Soft part colors in life: iris dark brown, bill black except for gray base of lower mandible, tarsus dark grayish-brown.

MEASUREMENTS (mm).—(Holotype, AMNH 820969 ♂; AMNH 820998 ♀; Kp 1955 am ♀; Kp 1955 an ♀): wing chord (73.0, 69.7, 69.9, 72.6); tail (51.6, 47.5, 48.4, 48.7); tarsus (17.0, 16.9, 15.4, 16.3); culmen from anterior edge of nostril (7.0, 6.6, 5.9, 6.3).

DISTRIBUTION.—Known only from the slopes of the Cerros del Sira, 9°26′S, 74°45′W, Departamento de Huánuco, Peru, from 1300 to 1570 m elevation.

ETYMOLOGY.—We take pleasure in naming this tanager for Allan R. Phillips in recognition of his accomplishments in clarifying the taxonomic relationships of neotropical birds.

SPECIMENS EXAMINED.—*Tangara phillipsi*: PERU: type locality (AMNH 1 ♂, 1 ♀; Zoological Museum, University of Hamburg [Kp] 2 ♀♀). *T. heinei*: VENEZUELA: Mérida (National Museum of Natural History, Smithsonian Institution [USNM] 1 ♂, 1 ♀); Aragua (USNM 1 ♂). COLOMBIA: Sierra Nevada de Santa Marta (USNM 10 ♂♂, 3♀♀; AMNH 9 ♂♂, 3 ♀♀); Antioquia (USNM 9 ♂♂, 6 ♀♀; AMNH 3 ♂♂, 2 ♀♀); Cundinamarca (USNM 2 ♂♂; AMNH 9 ♂♂, 5 ♀♀); Cauca (USNM 4 ♂♂, 3 ♀♀; AMNH 7 ♂♂, 3 ♀♀); Norte de Santander (USNM 1 ♂, 2 ♀♀); Huila (USNM 5 ♂♂, 1 ♀; AMNH 2 ♂♂); Nariño (USNM 1 ♂; AMNH 1 ♂, 1 ♀); Caldas (USNM 1 ♂). ECUADOR: Napo (AMNH 2 ♂♂, 2 ♀♀). *T. argyrofenges*: PERU: Amazonas (Louisiana State University 2 ♂♂, 1 ♀); San Martín (Academy of Natural Sciences of Philadelphia 1 ♂); Junín (Field Museum of Natural History [FMNH] 1 ♂). BOLIVIA: Cochabamba (FMNH 5 ♂♂, 1 ♀); Santa Cruz (Carnegie Museum of Natural History 4 ♂♂; FMNH 1 ♂; University of Michigan Museum of Zoology 1 ♂). *T. viridicollis*: ECUADOR:

Azuay (USNM 1 ♂). PERU: Huánuco: Cerros del Sira (AMNH 1 ♂); Cuzco (USNM 2 ♂♂, 2 ♀♀).

REMARKS

Description of females.—The three female specimens, all collected on 24 July 1969, vary only slightly in color. The crown is dull bluish-green to grayish-blue with a scaled appearance caused by the exposed dark feather bases. Back, rump, upper tail coverts, sides, and flanks are shining golden green (darker, less yellow than in female *T. argyrofenges*). The pattern of the wings and tail is similar to that of the male, with grayish-blue being replaced with shining green. Under-wing coverts are white, tinted slightly with pale yellow. Feather tips of the chin, throat, auriculars and upper breast are bifurcated and bluish-green, contrasting with gray feather bases and forming an indistinct pectoral belt. The lower breast and belly are bluish-gray, becoming lighter near the center of the lower belly. Tibial feathers are grayish-white. The under tail coverts are greenish-gray with broad cream-colored borders.

Ecology.—*Tangara phillipsi* was a fairly common member of mixed-species flocks in the cloud forest canopy and was observed at heights of 11–25 m above the forest floor. It occurred in canopy flocks with the tanagers *T. arthus* (Golden Tanager), *T. cyanotis* (Blue-browed Tanager), *T. nigroviridis* (Beryl-spangled Tanager), *T. xanthocephala* (Saffron-crowned Tanager), *Piranga leucoptera* (White-winged Tanager), *Calochaetes coccineus* (Vermilion Tanager), *Anisognathus flavinucha* (Blue-winged Mountain-Tanager), *Chlorochrysa calliparaea* (Orange-eared Tanager), *Euphonia xanthogaster* (Orange-bellied Euphonia), *Diglossa glauca* (Deep-blue Flower-piercer), and *Cyanerpes caeruleus* (Purple Honeycreeper), as well as with *Pachyramphus albogriseus* (Black-and-white Becard) and *Philydor erythrocercus* (Rufous-rumped Foliage-gleaner). There were no obvious behavioral features that differentiated *T. phillipsi* from the 4 other *Tangara* species with which it was observed. Three specimens of *T. phillipsi* were caught together in a mist net strung near the ground, but mist-netting would not be expected to provide an effective means of sampling abundance of this species because of its arboreal habits. The two specimens prepared by Weske (AMNH 820969, testes 1.5 mm, skull ossified, weight 20.8 g; AMNH 820998, ovary 6 mm, skull ossified, 20.3 g) appear to be adult by skull ossification and plumage criteria, although the gonads did not indicate breeding activity. Skull ossification data were not recorded on the labels of the females prepared by Maria Koepcke (Kp 1955 an, ovary 6 × 4 mm, 19.2 g; Kp 1955 am, ovary 7 × 5 mm, 16.8 g). The wings and tail of these 2 females are rounded and

slightly worn, and the body plumage is perceptibly duller and more lax in texture than the AMNH female, suggesting that they may be immatures less than a year old; however, their wing and tail measurements are longer than those of the AMNH female.

DISCUSSION

The ancestor-descendant sequence of the evolution of plumage pattern and color within *Tangara* and related genera (*Iridophanes, Chlorochrysa*) is unknown. Certain features such as the club-tipped, waxy feathers in *Chlorochrysa* are probably synapomorphic. Other modifications (e.g., opalescent, "metallic," and iridescent plumage) may have arisen several times within the Emberizines and are not very useful in determining relationships within *Tangara.*

On the basis of plumage, however, a monophyletic "black-capped" species complex (*T. heinei* superspecies [*T. heinei, T. phillipsi*], *T. argyrofenges* [Green-throated Tanager], and *T. viridicollis* [Silvery Tanager]) is defined by several characters, the combination of which is unique among *Tangara*: (1) marked sexual dichromatism; (2) black crown and forehead in males; (3) contrasting throat patch in males; and (4) opalescence on the mantle, sides, and flanks of males. *Tangara cyanoptera* (Black-headed Tanager), sympatric with *T. heinei* in the Sierra Nevada de Santa Marta and Serranía de Perijá in northern Colombia, is the only other sexually dichromatic species of *Tangara* with a black cap or hood. The male of *T. cyanoptera* has a black hood and opalescent mantle, and the Tepui subspecies, *T. c. whitleyi,* has unmarked black wings, a character shared only with *T. argyrofenges* within the genus. This superficial resemblance and the peripheral distribution of *T. cyanoptera* suggest that it may be more closely related to the "black-capped" species complex than are other members of the genus. Because synapomorphies of plumage characters within the "black-capped" group cannot be determined, the cladistic relationship among taxa is uncertain. *T. heinei, T. argyrofenges,* and *T. viridicollis* exhibit only subtle geographic variation in plumage pattern and color, none of which "clines" toward the appearance of *T. phillipsi* (pers. obs.).

The present day distributions of *T. phillipsi* and *T. argyrofenges* appear to be relictual. *T. argyrofenges* is known from three widely separated regions along the eastern slope of the Andes between 5° and 18° S latitude: (1) the northern spur-like terminus of the Eastern Cordillera in the Departamentos de Amazonas and San Martín, Peru; (2) Conchapen Mountain (Yurinaqui Alto), 5000 ft (1525 m), an outlying ridge in the Departamento de Junín, Peru; and (3) the "Yungas" of the Departamentos de

La Paz, Cochambamba and Santa Cruz, Bolivia. The absence of *T. argyrofenges* in several well-collected localities (e.g., Cordillera Carpish, Cordillera Vilcabamba) lying between known populations indicates that its patchy distribution is not a sampling artifact.

Terborgh and Weske (1975), Terborgh (1977), and Fitzpatrick et al. (1977) suggested that interspecific competition may be reduced in the depauperate avian communities found on Andean outliers. Although the ecological relationships of *Tangara* are imperfectly known, we guess that competition would be most intense between closely related species. The pattern of distributional overlap within the "black-capped" complex provides little evidence to support or reject this hypothesis. A single subadult specimen (AMNH 821010 ♂, 15.7 g, collected 13 July 1969) of *T. viridicollis,* the only "black-capped" *Tangara* throughout most of the Peruvian Andes, was mist-netted in the Cerros del Sira in the same net lines that captured *T. phillipsi.* As no other individuals were observed or netted anywhere in the Sira, *T. viridicollis* is either rare in this locality or the unique specimen represents a wanderer from farther downrange or from the main Andes. *T. viridicollis* is syntopic with the Peruvian populations of *T. argyrofenges.* At least 5 other species of *Tangara* (*arthus, xanthocephala, cyanotis, nigroviridis, vassorii*) are known to occur sympatrically with all Peruvian populations of *T. phillipsi* and *T. argyrofenges* (pers. obs.), and 5 additional species of *Tangara* (*parzudakii, ruficervix, punctata, chrysotis, labradorides*) are known to occur sympatrically with at least one of those populations.

T. heinei, the taxon exhibiting the most overall similarity to *T. phillipsi,* does not occur sympatrically with other "black-capped" species—the southernmost population of *T. heinei* (Río Oyacachi, Ecuador) is apparently separated from the only known population of *T. phillipsi* by a gap of 1100 km. This suggests that the 2 taxa have been isolated from reciprocal gene flow for a considerable period.

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COLOR PLATE

The Frontispiece painting has been made possible by an endowment established by George Miksch Sutton. The painting is by Morton L. Isler.

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EFFECT OF CHANGES IN REGIONAL FOREST ABUNDANCE ON THE DECLINE AND RECOVERY OF A FOREST BIRD COMMUNITY

Robert A. Askins and Margarett J. Philbrick[1]

Abstract.—Bird populations were monitored for 32 years in a 23-ha tract of hemlock-hardwood forest. Between 1953 and 1976 the total abundance of long-distance migrants declined significantly and four species disappeared, but after 1976 both the total abundance and the number of species increased. Multiple regression analysis shows that the abundance of long-distance migrants was negatively related to abundance of bird species characteristic of suburban habitats and positively related to the amount of forest within 2 km of the study area. The decline in long-distance migrants before 1976 occurred when suburban species were increasing and nearby forest was destroyed. The increase after 1976 is best explained by reforestation in the surrounding area because suburban birds were still increasing. A diversity of forest species, including many long-distance migrants, became established in the reforested areas. This pattern suggests that immigration from nearby forests is important in maintaining the abundance of long-distance migrants. *Received 22 Jan. 1986, accepted 10 July 1986.*

Long-term censuses of bird populations in six forest preserves in eastern North America reveal a substantial decline in both the species richness and density of migratory, forest-dwelling passerines during the past 20–30 years (Robbins 1979, Butcher et al. 1981, Leck et al. 1981, Serrao 1985). Many of the same species have declined in all of these preserves. Red-eyed Vireo, Black-throated Green Warbler, American Redstart, Ovenbird, and Hooded Warbler (scientific names are in Table 1) have decreased by 45–100% at sites where they were originally present. All sites are small urban and suburban preserves (generally <100 ha) that are isolated from other forests. Although little habitat change or direct human disturbance has occurred within the preserves, in almost all cases surrounding forest was destroyed during the period, thereby increasing the isolation of the preserves.

A greater proportion of edge habitat in small forests leads to higher rates of nest predation and brood parasitism (Gates and Gysel 1978, Brittingham and Temple 1983, Wilcove 1985), and may result in competition with "suburban" species (i.e., species that are common in edge habitat and wooded residential areas; Butcher et al. 1981). Also, bird species may disappear because particular microhabitats are absent in a small forest (Karr 1982) or because the small populations characteristic

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of small forests are prone to local extirpation as a result of stochastic population changes (Diamond 1984). The degree of isolation from other forests may be important because nearby forests may serve as sources of immigrants to bolster declining populations, thus offsetting some of the effects of small size (Brown and Kodric-Brown 1977, Lynch and Whigham 1984). Despite this, the importance of the isolation of preserves for highly mobile animals like birds has been questioned by some researchers (McCoy 1982, Ambuel and Temple 1983). Also, Briggs and Criswell (1979) and Rappole et al. (1983) argue that the destruction of wintering habitat in the Neotropics may be the primary cause of population declines in the temperate zone.

The decline in forest bird species is particularly well documented for the Connecticut Arboretum (New London, Connecticut, USA), where periodic breeding bird censuses and vegetation surveys have been conducted since 1953. Butcher et al. (1981) describe the steep decline in forest birds between 1964 and 1976, a period when forest immediately adjacent to the study area was cut down for commercial and highway construction. Five species disappeared from the study area, and the density of three other species dropped markedly. Here we report the results of breeding bird censuses made in the same study area between 1982 and 1985, at a time when the density and species richness of forest birds had increased in the area since 1976. We suggest that this apparent recovery of the forest bird community is associated with a net increase in the amount of forest in the immediate vicinity of the study area.

STUDY AREAS

The hemlock-hardwood study area is a 23.1-ha section of the Bolleswood Natural Area in the Connecticut Arboretum at Connecticut College, New London, Connecticut (41°23′N, 72°07′W). The site is in a 61-ha tract of contiguous forest and is bisected by an intermittent stream in a small ravine. The topography is undulating, with a maximum elevation of 70 m. Hemlock (*Tsuga canadensis*) and several species of oaks (*Quercus rubra, Q. alba, Q. velutina,* and *Q. coccinea*) dominate the canopy (Niering and Goodwin 1962), which consists of large trees that survived a hurricane in 1938, and small trees that have grown up since then.

Intensive vegetation surveys have been completed along 4 permanent transects every 10 years since 1952 (Niering and Goodwin 1962, Hemond et al. 1983). The major trends have been an increase in the total basal area of trees (from 20 m^2 ha^{-1} in 1952 to 37 m^2 ha^{-1} in 1982) and a decrease in the density and cover of shrubs. The cover of the two dominant species in the shrub layer, *Kalmia latifolia* and *Smilax rotundifolia,* declined by more than 50% between 1952 and 1972. Gypsy moths (*Lymantria dispar*) caused extensive defoliation of the oak forest in 1982 and moderate defoliation in 1983.

Bird populations and vegetation were also monitored at a second site (the old-field study area) adjacent to the hemlock-hardwood site. This 6.5-ha plot was an open field and low thicket in 1952 (Niering and Goodwin 1962). By 1976 it was largely covered with young

forest and high-shrub thicket (Butcher et al. 1981). The transition to young forest has continued since (Niering, unpubl. data).

We completed bird surveys in a third tract (Bolles Road study area) north of the hemlock-hardwood study area on the opposite side of a paved road. This 124-ha tract is predominantly young deciduous forest with small areas of thicket and red maple swamp. Much of the area had been farmland before 1945 (Goodwin 1982).

METHODS

Bird populations in the hemlock-hardwood and old-field study areas were estimated using the spot-mapping technique (International Bird Census Committee 1969). Population estimates from 1982 to 1985 were based on 10 censuses made each year between 10 May and 8 July between 05:00 and 08:00 EDT. Total coverage per year during this period ranged from 38 to 46 h for the two study sites. From 1953 to 1976, censuses were made at approximately the same time of day and during the same weeks of the breeding season. Number of visits and coverage were also similar except for the first two censuses (1953, 1955), which involved fewer visits (7–8) and less coverage (25–32 h). Although this could result in lower estimated densities for these years (Engstrom and James 1984), results of the spot-mapping technique are robust in the range of 7–10 visits (Svensson 1978). Fractional territories were not recorded until 1973, and this could lead to somewhat higher estimates for the earlier censuses.

The spot-mapping technique is generally considered the most accurate of the standard census methods for territorial passerines (Robbins 1978). The data for this study were collected and interpreted by several observers. Best (1975) has argued that this can lead to inaccuracies, but Enemar et al. (1978) and Robbins (1978) have shown that experienced observers can obtain consistent results when they census the same plot independently.

Bird densities were estimated for the Bolles Road study areas with strip transect surveys. Singing males were mapped on a transect (1.8 km long × 100 m wide) in 1982 and 1983 to estimate the relative abundance of breeding species. Surveys were made 2–3 times during the breeding season (23 May–17 July) between 05:30 and 09:00 EDT.

We determined the changes in total area of forest within 2 km of the center of the hemlock-hardwood study area (regional forest area) from aerial photographs (1:12,000–1:20,000 contact prints for 1951, 1965, 1975, and 1980; Natural Resources Center, Connecticut Department of Environmental Protection). For these purposes forest was defined as vegetation with a closed canopy of trees. This measure of regional forest area was used because it was an effective predictor of forest-interior bird densities for 46 forest tracts within 40 km of the study area (Askins, Philbrick, and Sugeno, unpubl. data).

Multiple regression analysis was used to determine which variables were the best predictors of population change. Previous studies indicated that forest fragmentation primarily affects forest-interior birds and long-distance migrants (Whitcomb et al. 1981, Blake and Karr 1984). We therefore analyzed the following groups of species separately: forest-interior species—territories normally restricted to interior of forest; interior-edge species—territories commonly occur both in forest interior and forest edge; edge species—primarily use forest edge or require open habitats for foraging (combines edge and field edge categories of Whitcomb et al. 1981); long-distance migrants—move to Neotropics for the winter; short-distance migrants—move to southern temperate zone or subtropics for winter; and permanent residents—remain in breeding area in winter. Classification of species into these groups is based upon Butcher et al. (1981), Whitcomb et al. (1981), and Freemark and Merriam (1986).

Combinations of 2 to 3 of the following independent variables were used in regression

analyses of population change: regional forest area, number of Brown-headed Cowbirds, number of avian nest predators (Blue Jay, American Crow, Common Grackle), and number of "suburban" species (Butcher et al. 1981). Although cowbirds and the nest predators are normally included in the suburban category, they were not included during regression analysis because they were considered separately.

RESULTS AND DISCUSSION

Between 1953 and 1976 eight species of forest-dwelling birds disappeared or declined in the hemlock-hardwood study area (Butcher et al. 1981). Seven of these species (Eastern Wood-Pewee, Red-eyed Vireo, Black-throated Green Warbler, American Redstart, Ovenbird, Hooded Warbler, Canada Warbler) are long-distance migrants (Table 1), and there was a significant decline in the total abundance of long-distance migrants (Spearman rank correlation, $r_s = -0.86$, $P < 0.05$) (Fig. 1). Short-distance migrants and permanent residents tended to increase in abundance during this period, but these trends were not significant ($P > 0.05$). The total abundance of both forest-interior and interior-edge species showed a nonsignificant tendency to decline ($P > 0.05$) (Fig. 2), while edge species increased significantly ($r_s = 0.89$, $P = 0.02$).

Between 1976 and 1985 there was an increase in the abundance of some of the long-distance migrants that had previously declined (Red-eyed Vireo, Ovenbird, Hooded Warbler). Moreover, Eastern Wood-Pewee and American Redstart, which had previously disappeared, were again present (Table 1); and Worm-eating Warbler became established for the first time (but was again absent in 1985). The total abundance of long-distance migrants did not increase significantly during this period ($P > 0.05$), but this is due to a decline in abundance after a peak in 1983 (Fig. 1). Forest-interior and interior-edge species also tended to increase in abundance after 1976 (Fig. 2), but these trends are not significant ($P > 0.05$). However, the density of Red-eyed Vireo (originally the most abundant long-distance migrant) did increase significantly ($r_s = 1.0$, $P = 0.05$) (Table 1).

The decline in abundance of long-distance migrants occurred at the same time that the amount of forest near the study area was reduced, whereas the subsequent, apparent increase in abundance occurred when the amount of nearby forest increased. Regional forest area decreased from 418 ha to 363 ha between 1951 and 1975 due primarily to commercial development south of the study area, and increased to 464 ha by 1985 due to growth of forest on abandoned farmland in and around the Bolles Lane and old-field study areas.

In multiple regression analyses the abundance of all long-distance migrants and of long-distance migrants in the forest-interior and interior-

edge categories (hereafter referred to as forest long-distance migrants or FLM) were both used as dependent variables. We report on the results for FLM species because this group is more pertinent to a discussion of changes in forest bird populations. The results for the two variables, however, were similar.

Regression analysis showed that between 1953 and 1985 the total abundance of FLM species was positively correlated with regional forest area ($F = 10.2$, $P < 0.05$) and negatively correlated with abundance of suburban species ($F = 12.8$, $P < 0.02$). The other independent variables (number of cowbirds and number of avian nest predators) did not have significant partial regression coefficients.

The positive relationship between the abundance of long-distance migrants and the amount of forest within 2 km of the study area is consistent with the hypothesis that the composition of forest bird communities is directly affected by the degree of isolation from similar communities that might serve as a source of immigrants. Between 1953 and 1985 the abundance of forest long-distance migrants increased significantly in abandoned farmland of the old-field study area ($r_s = 0.81$, $P < 0.01$); by 1982, nine species were present (Fig. 3). Aerial photos show that the sequence of vegetation change in the Bolles Road study area was similar to the sequence in the old-field study area. By 1982 this northern tract was a mosaic of young and older forest, and a large number of species of forest birds (including the species that had increased in the hemlock-hardwood study area) were detected on transect surveys of the tract in 1982 and 1983 (Table 2). Thus, over the course of our study, the hemlock-hardwood study area was becoming less isolated from other forest bird communities.

The abundance of FLM species declined during a period of deforestation and increased during a period when forest grew up and forest bird communities became established nearby. Both the reduction and increase in regional forest area were small (13% and 28%, respectively), but in both cases tracts immediately adjacent to the study area were affected. The proximity of other forest bird communities could determine the rate of dispersal into the study area, which in turn could determine whether some species maintain viable populations or become reestablished.

The negative relationship between suburban species and FLM migrants is consistent with the hypothesis that the influx of suburban species into small forests has a negative impact on migratory forest birds (Butcher et al. 1981, Whitcomb et al. 1981). Between 1953 and 1985 the density of suburban species increased ($r_s = 0.90$, $P < 0.001$) while that of FLM migrants declined ($r_s = -0.74$, $P < 0.05$). Abundance of suburban species was not correlated with regional forest area ($r_s = 0.52$, $P > 0.05$) and was a significant predictor of abundance of FLM migrants even when regional

TABLE 1

NUMBER OF TERRITORIAL MALES RECORDED IN THE 23-HA HEMLOCK-HARDWOOD STUDY AREA OF THE CONNECTICUT ARBORETUM DURING A 32-YEAR PERIOD

Species	1953	1955	1959	1961	1964	1973	1976	1982	1983	1984	1985
Forest-interior species											
Long-distance migrants											
Broad-winged Hawk (*Buteo platypterus*)	0	0	0	1	0	0	1	0.5	1	0	0
Acadian Flycatcher (*Empidonax virescens*)	0	0	0	0	0	0	0	2	0	0	0
Veery (*Catharus fuscescens*)	9	6	6	8	12	10	9	15.5	11.5	13.5	11.5
Magnolia Warbler (*Dendroica magnolia*)	0	1	0	0	0	0	0	0	0	0	0
Black-throated Green Warbler (*D. virens*)	3	0	3	1	6	0	0	0	0	0	0
Black-and-white Warbler (*Mniotilta varia*)	14	10	4	4	10	5	6	6.5	9.5	9	5.5
American Redstart (*Setophaga ruticilla*)	0	6	3	7	1	0	0	0	1	0.5	0
Worm-eating Warbler (*Helmitheros vermivorus*)	0	0	0	0	0	0	0	1	1	1	0
Ovenbird (*Seiurus aurocapillus*)	11	11	9	12	16	11	5	13.5	15	10	11.5
Louisiana Waterthrush (*S. motacilla*)	1	0	0	0	1	0	1	2	2	2	1
Hooded Warbler (*Wilsonia citrina*)	5	13	17	9	7	1	0.5	0	1.5	2.5	4
Canada Warbler (*W. canadensis*)	7	2	2	1	2	0	0	0	0	0	0
Scarlet Tanager (*Piranga olivacea*)	5	4	5	3	2	3	5	4.5	6.5	4	3.5
Short-distance migrants											
Winter Wren (*Troglodytes troglodytes*)	0	0	0	0	0	1	0	0	0	0	0
Permanent residents											
Barred Owl (*Strix varia*)	0	0	0	0	0	0	0	2	1	1	1
Hairy Woodpecker (*Picoides villosus*)	0	0	0	2	1	0	1	1	2	2	1.5
White-breasted Nuthatch (*Sitta carolinensis*)	0	0	0	0	1	1	0	3	2	2	3.5
Brown Creeper (*Certhia americana*)	0	0	0	0	0	0	0	0	0	0	0.5

TABLE 1
CONTINUED

Species	1953	1955	1959	1961	1964	1973	1976	1982	1983	1984	1985
Interior-edge species											
Long-distance migrants											
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	0	0	0	0	0	0	0	1	0	0.5	0
Yellow-billed Cuckoo (*C. americanus*)[a]	0	0	0	0	0	1	0	1	0.5	0	0
Eastern Wood-Pewee (*Contopus virens*)[a]	3	1	1	3	3	0	0	3.5	1	3	2
Great Crested Flycatcher (*Myiarchus crinitus*)	0	0	1	3	2	4	4	4.5	4	5	3
Wood Thrush (*Hylocichla mustelina*)[a]	7	10	12	9	1	7	5	5.5	6.5	2	2.5
Red-eyed Vireo (*Vireo olivaceus*)	20	22	16	21	17	2	4	10	13	14	15
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	0	0	0	0	0	0.5	0	0.5	0	0	0
Short-distance migrants											
Northern Flicker (*Colaptes auratus*)[a]	2	1	1	1	2	2.5	0	1.5	1	0.5	1
Eastern Phoebe (*Sayornis phoebe*)	1	1	1	0	0	0	1	2	0	1	1
Gray Catbird (*Dumetella carolinensis*)[a]	9	8	6	9	10	9.5	10	7.5	9.5	9.5	9.5
White-eyed Vireo (*V. griseus*)	0	1	2	0	0	0	1	2	0	0.5	2.5
Common Yellowthroat (*Geothlypis trichas*)	5	2	2	2	3	1	2	3.5	3.5	6	2
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	7	9	15	15	13	10	7	5.5	10	4.5	7.5
Permanent residents											
Ruffed Grouse (*Bonasa umbellus*)	1	1	1	0	2	1	0	0	0	0	0
Downy Woodpecker (*Picoides pubescens*)[a]	0	0	0	0	0	2	0	2.5	2.5	2	2
Blue Jay (*Cyanocitta cristata*)[a,b]	1	2	4	4	3	7	2	5.5	4	4	1
Black-capped Chickadee (*Parus atricapillus*)[a]	3	2	4	5	5	7	2	10	11.5	11.5	11.5
Tufted Titmouse (*P. bicolor*)[a]	0	0	0	0	0	0	5	7.5	8	9.5	9.5
Carolina Wren (*Thryothorus ludovicianus*)[a]	0	1	1	0	0	0	0	0	0	0	0
Northern Cardinal (*Cardinalis cardinalis*)[a]	0	0	0	0	1	1	1.5	7	4	3	3

TABLE 1
CONTINUED

Species	1953	1955	1959	1961	1964	1973	1976	1982	1983	1984	1985
Edge species											
Long-distance migrants											
Whip-poor-will (*Caprimulgus vociferus*)	1	0	2	1	0	0	0	0	0	0	0
Eastern Kingbird (*Tyrannus tyrannus*)	0	0	0	0	0	0	0	0	0	0.5	0
Blue-winged Warbler (*Vermivora pinus*)	1	1	0	0	3	0	1	2	2.5	3	1.5
Chestnut-sided Warbler (*Dendroica pensylvanica*)	1	1	0	0	3	1.5	0	2.5	1.5	1.5	1.5
Prairie Warbler (*D. discolor*)	0	0	1	0	0	0	0	0	0	0	0
Indigo Bunting (*Passerina cyanea*)	0	0	0	0	0	0	1	0	0	0	0
Northern Oriole (*Icterus galbula*)[a]	0	0	0	0	0	2.5	4	1.5	1	0.5	0
Short-distance migrants											
Mourning Dove (*Zenaida macroura*)[a,b]	0	0	0	0	2	0	0	1.5	0	0	0
House Wren (*Troglodytes aedon*)[a]	1	1	2	4	8	5	8.5	6.5	7	6	10
American Robin (*Turdus migratorius*)[a]	0	0	0	2	1	1	1	0	0	0	0
Brown Thrasher (*Toxostoma rufum*)[a]	0	0	2	0	1	3	1	0	0	0	0
Chipping Sparrow (*Spizella passerina*)	0	0	0	0	0	0	0	0	0	1	0
Song Sparrow (*Melospiza melodia*)	0	0	0	0	0	0	0	0	1	0	0
Red-winged Blackbird (*Agelaius phoeniceus*)	0	0	0	0	1	4	1	2	2	0	0
Common Grackle (*Quiscalus quiscula*)[a,b]	0	0	0	1	0	0	0	0	0	0	0
Brown-headed Cowbird (*Molothrus ater*)[a,c]	0	0	0	0	1	0	0	9.5	2.5	1.5	2
	(0)	(6)	(1)	(1)	(2)	(1)	(2)	(69)	(33)	(22)	(13)

TABLE 1
CONTINUED

Species	1953	1955	1959	1961	1964	1973	1976	1982	1983	1984	1985
Permanent residents											
Northern Bobwhite (*Colinus virginianus*)	0	1	0	0	0	0	0	0	0	0	0
American Crow (*Corvus brachyrhynchos*)[a]	0	0	2	2	1	0	0	0	0	2.5	1

[a] Suburban species (i.e., characteristic of wooded residential areas; Butcher et al. 1981).
[b] Because males do not defend a large territory, the estimated number of breeding pairs is indicated.
[c] Repeated observations of cowbirds in one area may indicate a female territory, but this is difficult to confirm as females are more secretive and silent than males (Dufty 1982). Therefore, to provide another measure of abundance, the total number of separate observations of cowbirds is shown for each year (in parentheses).

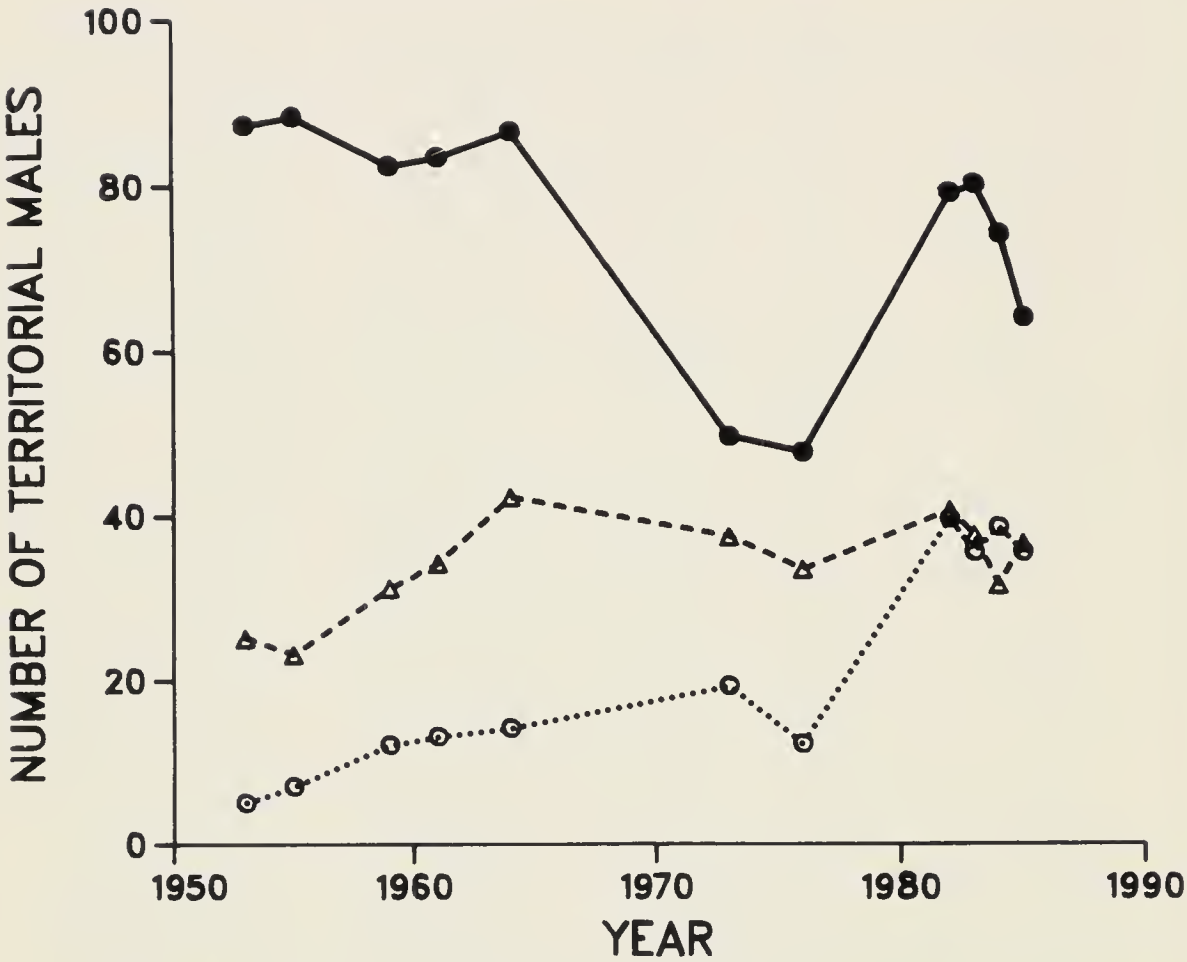

FIG. 1. Change in total population for long-distance migrants (solid line), short-distance migrants (dashed line), and permanent residents (dotted line).

forest area was controlled for in multiple regression analysis. Suburban species increased from 46 to 57 territorial males between 1976 and 1985 as regional forest area increased.

Most of the increase in abundance of suburban birds was due to three species: Black-capped Chickadee, Tufted Titmouse, and House Wren (Table 1). All are foliage-gleaning insectivores, and thus are possible competitors with the FLM species that declined, most of which are also foliage-gleaners (six species of vireos and wood warblers). Populations of Black-capped Chickadee and Tufted Titmouse appear to have increased regionally, perhaps as a result of suburban bird feeders (Kricher 1981). Also, Tufted Titmouse expanded its range northward into Connecticut during the period (Kricher 1981, Loery and Nichols 1985). A regional increase in these foliage-gleaners could lead to a decline in FLM species with similar feeding behavior, but the FLM decline is not necessarily related causally to the increase in suburban birds. Suburban species may have increased due to competitive release after the FLM decline (Whit-

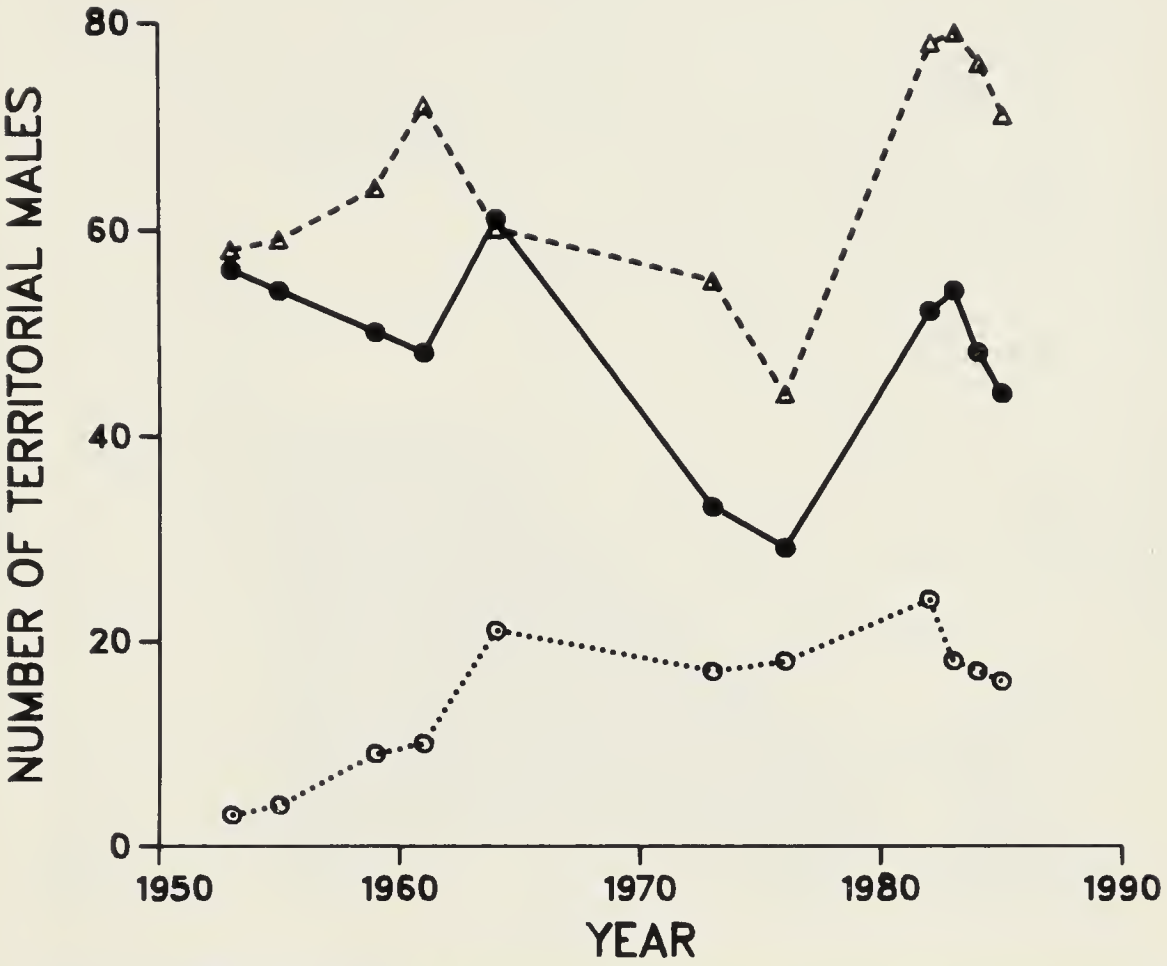

FIG. 2. Change in total population for forest-interior species (solid line), interior-edge species (dashed line), and edge species (dotted line).

comb et al. 1981), or both groups may have been responding to habitat change in and around the study area.

The shrub layer became less dense between 1953 and 1973 (Hemond et al. 1983), and this is a potential factor in the decline of American Redstart, Canada Warbler, and Hooded Warbler, species that nest and feed in this layer and the understory (Bent 1953, Anderson and Shugart 1974, Seidel and Whitmore 1982). The Hooded Warbler population increased between 1976 and 1985 as the shrub layer became even less dense (Niering, unpubl. data), so thinning of the shrub layer does not entirely account for its previous decline. Habitat change may account for the decline of the other two species, which showed little or no increase during this period. However, the abundance of FLM migrants is still related to both regional area and abundance of suburban species when these two species are not included in the analysis ($F > 10$, $P < 0.05$ for both variables).

Red-eyed Vireo, Ovenbird, and Black-throated Green Warbler declined

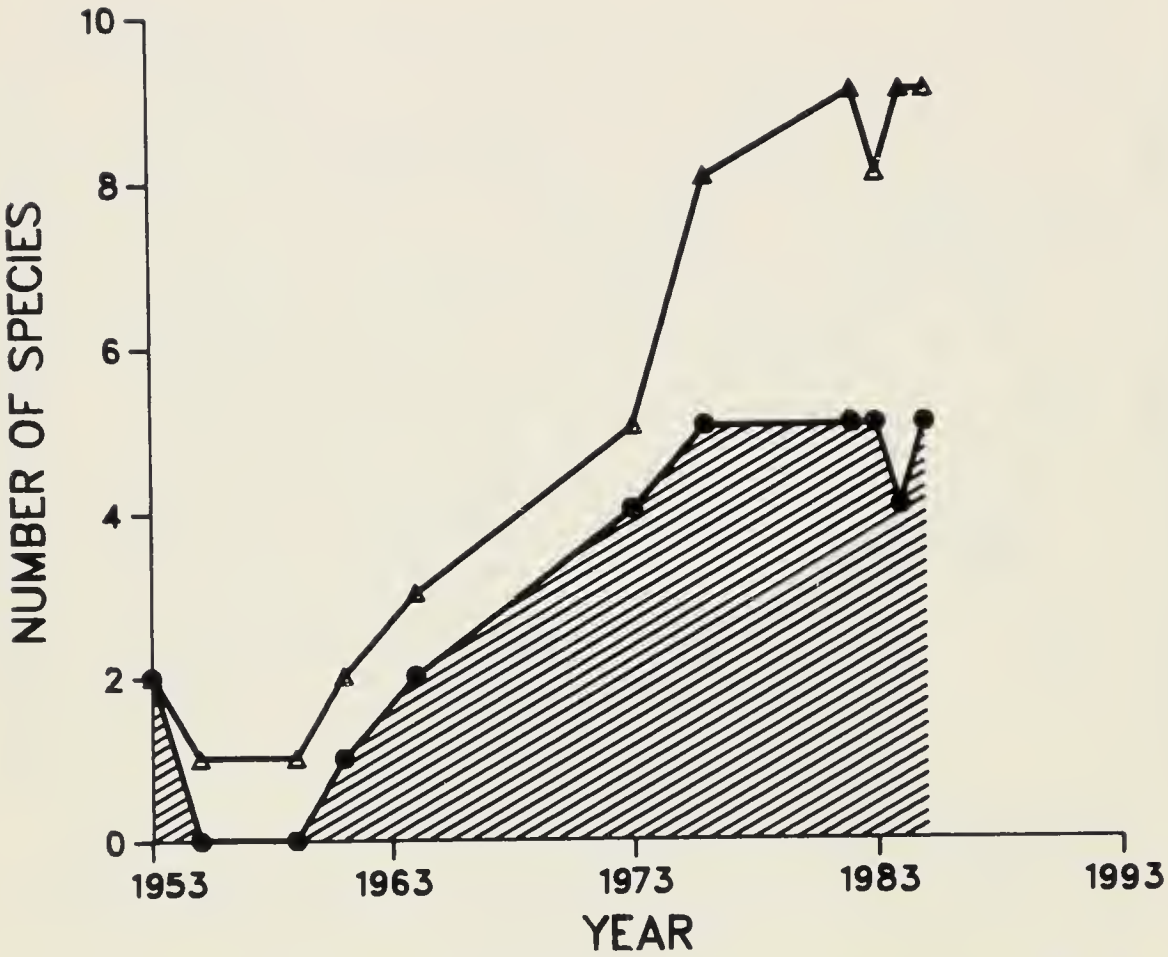

FIG. 3. Change in the number of species of interior-edge birds (unshaded) and forest-interior birds (shaded) in the old-field study area during a period of transition from open field and low thicket to young forest.

despite an apparent increase in favorable habitat (closed canopy forest, Clark et al. 1983). In fact, between 1953 and 1985 the total abundance of FLM species was negatively correlated with total basal area of trees ($r = -0.66$, $P < 0.05$), indicating that these species declined despite the maturation of the forest (i.e., larger trees and an associated decrease in the density of trees and shrubs; Hemond et al. 1983).

Brittingham and Temple (1983) argue that brood parasitism by Brown-headed Cowbirds may be a major factor in the decline of forest bird populations in small forest patches in the eastern United States. Brown-headed Cowbird abundance was not significantly related to FLM abundance in the Connecticut Arboretum. Cowbird abundance was low during the period of FLM decline, but was considerably higher during the 1980s (perhaps due to high densities of gypsy moth caterpillars, Smith and Lautenschlager 1981), when FLM birds had increased. Only the small

TABLE 2
COMPARISON OF POPULATION DENSITIES OF LONG-DISTANCE MIGRANTS IN THE HEMLOCK-HARDWOOD AND BOLLES ROAD STUDY AREAS

	Estimated density (males or pairs/10 ha)			
	Hemlock-hardwood[b]		Bolles Road	
Species[a]	1982	1983	1982	1983
Eastern Wood-Pewee	1.5	0.4	1.7	1.1
Red-eyed Vireo	4.3	5.7	6.1	6.7
American Redstart	0	0.4	0	0
Worm-eating Warbler	0.4	0.4	0.6	1.1
Ovenbird	5.9	6.5	1.7	5.0
Hooded Warbler	0	0.7	2.2	2.2

[a] Only FLM species that increased in abundance in the hemlock-hardwood study area between 1976 and 1985 are included.
[b] The hemlock-hardwood study area includes 23 ha and the Bolles Road study area includes 124 ha.

decline in long-distance migrant abundance in 1984–1985 (Fig. 1) is likely to be due to cowbird parasitism.

High nest predation rates in small, suburban forests have been demonstrated experimentally (Wilcove 1985). Although the abundance of avian nest predators is not related to FLM abundance, we have no data on mammalian predators.

Our results suggest that the abundance of forest-dwelling, long-distance migrants is related to the abundance of suburban species and to regional forest area. Long-distance migrants declined during a period when suburban species were increasing and when forest close to the study area was destroyed. After 1976, however, the populations of several species of long-distance migrants increased. This partial recovery occurred during a period when the abundance of suburban species was still increasing, but when areas of thicket near the study area changed to young forest. Of the six forest tracts in the northeastern U.S. in which a general decline in forest birds has been documented during the past 20–30 years, the Connecticut Arboretum is the only site where populations of several species have recently recovered. It is also the only site for which reforestation in adjacent areas has been reported (Robbins 1979, Leck et al. 1981, Serrao 1985). This suggests that populations of many species are not self-sufficient in a small preserve, but instead are part of a larger, regional population (Ambuel and Temple 1983). Thus, extensive deforestation in the vicinity of a preserve may cause populations of these species to decline and might result in their extirpation.

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Wilson Bull., 99(1), 1987, pp. 22–37

FOREST OPENINGS AND THE DISTRIBUTION OF UNDERSTORY BIRDS IN A PUERTO RICAN RAINFOREST

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ABSTRACT.—From October 1983 through September 1984, 19 two-day mist-net censuses were conducted in a tabonuco (*Dacroydes excelsa*) forest in Puerto Rico to examine the species richness and composition of the understory avifauna in small treefall gaps, a larger powerline opening, and forest understory. We captured 531 birds representing 17 species. Although numbers of species captured in the three habitats were similar, numbers of captures differed among habitats. Of the 12 species with adequate sample size, 6 were captured significantly more often in at least one habitat of a pair (gap-forest, gap-powerline, powerline-forest). Analysis of all nets by Bray-Curtis ordination indicates that although gap and forest assemblages are distinct, both overlap with the powerline opening assemblage. Treefall gaps were probably too small and rare to support gap specialist birds, and differences between gap and forest assemblages can be attributed to the presence of canopy series that follow the canopy into or out of gaps. We therefore suggest that individual treefall gaps contribute to the composition and richness of understory bird assemblages in Caribbean forests by attracting canopy dwellers rather than by attracting gap specialists. *Received 17 May 1986, accepted 6 Aug. 1986.*

Small forest openings contribute to the structural heterogeneity of tropical forests and may influence composition and richness of the bird community (Stiles 1983). In a lowland forest in Panama, Schemske and Brokaw (1981) found that gap and forest understory bird assemblages were distinct, and that several species displayed preference for either gap or forest understory. These findings are consistent with previous studies, which suggest that tropical (continental) forest birds often show narrow habitat preference (Orians 1969, Terborgh and Weske 1969, Karr and Roth 1971, Pearson 1971, Terborgh 1971). Certain species show a preference for forest openings (Willis and Oniki 1972, Stiles 1975, Gradwohl and Greenberg 1980). In mature lowland forest in Peru, forest openings contained bird species characteristic of secondary habitats (Pearson 1971). Often the bird species found in forest openings and second growth areas also are observed in the forest canopy, but not in the surrounding forest understory (Orians 1969, Pearson 1971, Greenberg 1981). Our work investigates understory bird communities of gaps, a larger forest opening, and surrounding mature rainforest on the Caribbean island of Puerto Rico.

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For a variety of reasons, we did not expect to find many, if any, gap specialists in the avifauna of Puerto Rican rainforests. One principal reason is the comparative lack of gaps in the forest. The contribution of the gap phase to habitat heterogeneity varies within and among forests according to several factors (Garwood et al. 1979), including treefall frequency, size class distribution of treefall gaps, and regeneration time from gap to maturity. These factors are likely to be very different on islands such as Puerto Rico, where severe hurricanes occur approximately once every 10 years (Wadsworth and Englerth 1959). Caribbean island rainforests are specially adapted to withstand frequent hurricanes. The canopy of island rainforests is generally more even, lower in stature, and lacking in emergent crowns, as compared with lowland forests not exposed to hurricanes (Odum 1970, Doyle 1981). This relatively unbroken canopy of island rainforests may be maintained by trees that typically remain standing after death, and decompose without producing a large gap. Thus, the relatively homogeneous physiognomy of Caribbean island rainforests provides only small and rare habitats for potential gap specialist species.

A second reason for predicting fewer gap species in Puerto Rico is that numerous studies have suggested that island bird populations have broader habitat preferences than those on the mainland (Crowell 1962, MacArthur et al. 1966, Keast 1970, Diamond 1971, Cox and Ricklefs 1977). Thus it seems unlikely that avian gap specialists would be present in the Puerto Rican rainforests because of the tendency for island birds to use a wide range of habitats, and because of the limited production of gaps.

Our work takes advantage of the relatively well-known avifauna of the El Verde rainforest in eastern Puerto Rico (MacArthur et al. 1966, Recher and Recher 1966, Recher 1970, Kepler and Kepler 1970, Reagan et al. 1982) to study the distribution of birds in the understory of closed forest, small gaps, and a larger forest opening. We addressed the following questions: (1) Do treefall gaps or forest openings have an assemblage of birds different from or more diverse than that of intact forest understory? (2) Do particular bird species exhibit preferences between forest understory, small treefall gaps, and larger forest openings? (3) Is the assemblage of birds found in small treefall gaps a subset of the assemblage found in larger forest openings? (4) How do forest openings contribute to bird diversity in tropical island forests?

STUDY SITE

We captured birds in three habitats near the El Verde Field Station in the Caribbean National Forest in eastern Puerto Rico. The forest at El Verde has been well described (Odum and Pigeon 1970, Brown et al. 1983). It is classified as subtropical wet forest in the

Holdridge system and is a broad-leaved evergreen forest. The study site lies at an elevation of 350 m with moderately sloping topography, a permanent river to the north, and temporary streams running through the netting area. An average of 346 cm of rain falls per year with a slight dry season from December to April. During our study there was no rainfall in April or May of 1984 (vs an average of 58 cm for these two months). The dominant tree, tabonuco (*Dacryodes excelsa*) comprises as much as 35% of the forest canopy (Wadsworth 1951). Three tree strata are evident: a discontinuous upper layer at 24 m, a second continuous canopy at 20 m, and an understory. The understory is sparsely vegetated and has an open appearance due to the lack of branches to heights greater than half the height of most trees. Epiphytes, lianas, arborescent ferns, and understory palms are common.

METHODS

Three understory habitats, defined by their foliage height profiles and area, were sampled with mist nets. Six nets (12 m length, 30-mm mesh) were placed in treefall gaps, six in second growth in a powerline opening, and six in the understory of the surrounding natural intact forest. We use Brokaw's (1982) definition of a gap as "a vertical hole in the forest extending through the canopy to within 2 m of the forest floor." Four gaps >12 m long were censused, two of which were large enough to accommodate two nets. The mean gap area was 117 m^2 (range = 78–168 m^2). Nets were placed in the gaps to minimize visibility, but retain all of the net area within the gap. The gaps were surrounded by intact forest which had foliage height profiles similar to those of the forest understory nets. In this same area (Fig. 1), a powerline opening had been cut through the forest leaving a second growth strip 15 m wide and over 1.6 km long. Within this powerline cut, six nets were alternately placed across or parallel (in the center) to the long axis of the opening. Paired with the powerline nets were six forest understory nets set in the same compass direction as the corresponding powerline net and at least 15 m from the corresponding net and 10 from the edge of the powerline opening. Small temporary streams (dry from March through May) ran through all three habitats and under nets 3, 8, and C. Because the presence of water could influence capture rates, these nets are excluded from analysis unless specifically mentioned.

We determined foliage height profiles to quantify the vegetation surrounding the nets in each habitat, using the techniques of Karr (1971) and Schemske and Brokaw (1981). We established the six 12-m long transects parallel to each net at 0.5 m intervals on each side of the net. The presence or absence of vegetation within each of 13 height intervals was recorded at every 1 m along the transects. Height intervals (in meters) were 0–0.25, 0.25–0.50, 0.50–0.75, 0.75–1.00, 1.0–1.5, 1.5–2, 2–3, 3–5, 5–10, 10–15, 15–20, 20–25, and 25–30. To sample vegetation below 2 m, we recorded all vegetation that touched a vertical 1.5 cm × 2 m pole placed at each sampling point. For height intervals above 2 m we sighted along the vertical pole and recorded the presence or absence of vegetation in each height zone as determined by a rangefinder. For each net, we sampled at 156 points and calculated the percent cover for each height interval.

All nets were run for two days on each of 19 weekends (designated as netting sessions), at two or three-week intervals during a 12-month period from 8 October 1983 to 30 September 1984. Initially, netting was done every two weeks, but because of declining capture rates we switched to three-week intervals in December. This schedule was maintained until the end of the study, with the exception of April and May, when we returned to two-week intervals because of higher capture rates. Nets were open from dawn to dusk on both Saturday and Sunday of each netting session, and were checked every 1–2 h. The nets were closed for 7.5 h during the day on 10 June due to heavy rainfall. All captured birds were given unique color-band combinations except for hummingbirds and todies in which a combination of tail feathers were clipped.

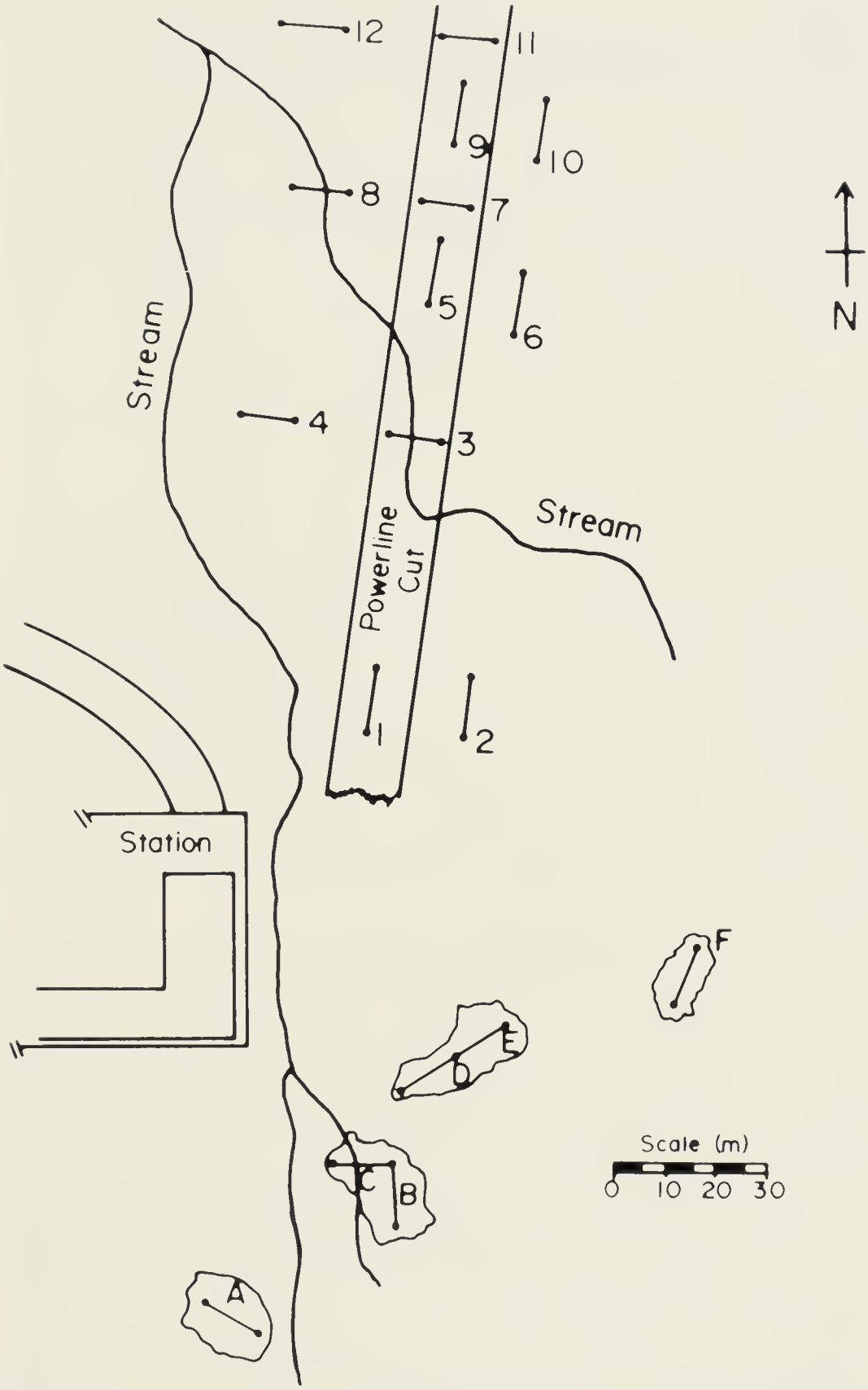

FIG. 1. Map showing the location of all nets at the El Verde research station, Puerto Rico. Treefall gap nets are shown with letters, nets in the powerline opening have odd numbers, and forest understory nets have even numbers.

A Friedman rank sums test based on distribution-free multiple comparisons (Hollander and Wolfe 1973:151) was used to compare the captures of a species among the three habitats when sample sizes were sufficient (Table 1). This test makes all possible pairwise comparisons among the three habitats while controlling for the experimentwise error rate within each species.

We used a polar ordination technique (Bray and Curtis 1957) as used by Beals (1960) and Schemske and Brokaw (1981) to examine whether the three different habitats support different assemblages of birds. With this technique, each net is considered to be a sample of the avifauna of one of the habitats. The relative similarity of the net samples can be determined by ordination of all nets with respect to bird composition. A percentage similarity (PS) matrix was used to construct the Bray-Curtis ordination:

$$PS = 100 - \tfrac{1}{2} \sum_{i=1}^{n} |P_{ai} - P_{bi}|$$

where P_{ai} and P_{bi} represent the percent individuals belonging to species i in samples a and b.

RESULTS

Vegetation profiles showed considerable differences between the forest understory and gap nets (Fig. 2). While much of the vegetation in the gaps was concentrated below 2 m, vegetation in the forest was thickest at 10–15 m. Gaps and powerline openings contained numerous low woody shrubs and herbs at net height, often with the branches of a few canopy trees extending into or alongside the gap. Generally, vegetation under the powerline was higher than that of gaps, which had a more even distribution throughout the height profile. The lower vegetation of the forest understory frequently was composed of palms which were rare in both the treefall gaps and powerline opening.

In 7524 net hours we recorded 531 captures representing 17 species in 10 families (Table 1). During October through February the overall capture rates remained relatively constant at an average of 0.06 captures/net-h. The rate increased from February to April, with a peak on April 14 of 0.14 captures/net-h. After April, rates declined to a low of 0.03 captures/net-h on 20 July. Much of this seasonal pattern was attributable to captures in the forest understory nets (range 0.0–0.12 captures/net-h) and powerline opening nets (range 0.03–0.23 captures/net-h). Gap nets showed a different pattern with a maximum peak of 0.14 captures/net-h on 18 November and a low of 0.01 captures/net-h on 30 June. Overall, we averaged 27.9 captures per netting session (range = 13–59) and 5.6 species per session (range = 4–10).

Total captures differed among the three habitats (Table 1). The 163 captures in the powerline nets were significantly more ($\chi^2 = 9.458$, $P < 0.005$) than the 112 captures in the gaps, which, in turn, were significantly more ($\chi^2 = 10.215$, $P < 0.005$) than the 69 captures in the forest. Whereas

Table 1

Total Captures over All Nets

Species	Number of captures[a]						Significance level[b]		
	Powerline		Treefall		Forest				
	A	B	A	B	A	B	P vs T	P vs F	T vs F
Bananaquit (*Coereba flaveola*)	161	76	69	45	25	23	$P < 0.05$	$P < 0.05$	$P < 0.05$
Puerto Rican Tody (*Todus mexicanus*)	34	20	34	28	9	5	N.S.	$P < 0.05$	$P < 0.05$
Puerto Rican Emerald (*Chlorostilbon maugaeus*)	33	17	18	13	13	10	N.S.	N.S.	N.S.
Ruddy Quail-Dove (*Geotrygon montana*)	21	20	9	8	23	19	$P < 0.05$	N.S.	$P < 0.05$
Green Mango (*Anthracothorax viridis*)	18	9	0	0	0	0	$P < 0.007$	$P < 0.007$	N.S.
Black-whiskered Vireo (*Vireo altiloquus*)	8	6	3	3	4	4	N.S.	N.S.	N.S.
Black-throated Blue Warbler (*Dendroica caerulescens*)	7	4	7	6	0	0	N.S.	N.S.	$P = 0.039$
Puerto Rican Bullfinch (*Loxigilla portoricensis*)	2	1	6	6	0	0	N.S.	N.S.	$P = 0.029$
Puerto Rican Tanager (*Neospingus speculiferus*)	5	3	0	0	2	2	N.S.	N.S.	N.S.
Louisiana Waterthrush (*Seiurus motacilla*)	2	2	0	0	4	2	N.S.	N.S.	N.S.
Red-legged Thrush (*Turdus plumbeus*)	2	2	1	1	1	1	N.S.	N.S.	N.S.
Pearly-eyed Thrasher (*Margarops fuscatus*)	1	1	1	1	1	1	N.S.	N.S.	N.S.
Black-faced Grassquit (*Tiaris bicolor*)	2	2	0	0	1	1	N.T.	N.T.	N.T.
Northern Parula (*Parula americana*)	1	0	1	1	0	0	N.T.	N.T.	N.T.
Black-throated Green Warbler (*Dendroica virens*)	0	0	0	0	0	1	N.T.	N.T.	N.T.
American Redstart (*Setophaga ruticilla*)	1	0	0	0	0	0	N.T.	N.T.	N.T.
Black-and-white Warbler (*Mniotilta varia*)	1	0	0	0	0	0	N.T.	N.T.	N.T.
Total	299	163	149	112	83	69			

[a] Number of captures per powerline opening, treefall gap, and forest understory nets. Captures within each habitat are divided into the totals for all nets in a habitat (A) and totals without the stream nets (B).

[b] Significance levels for Friedman rank sums tests (see text) for pairwise comparisons among the three habitats with stream nets excluded (B only). P = powerline, T = treefall gap, and F = forest understory. N.S. = $P > 0.05$; N.T. = no test.

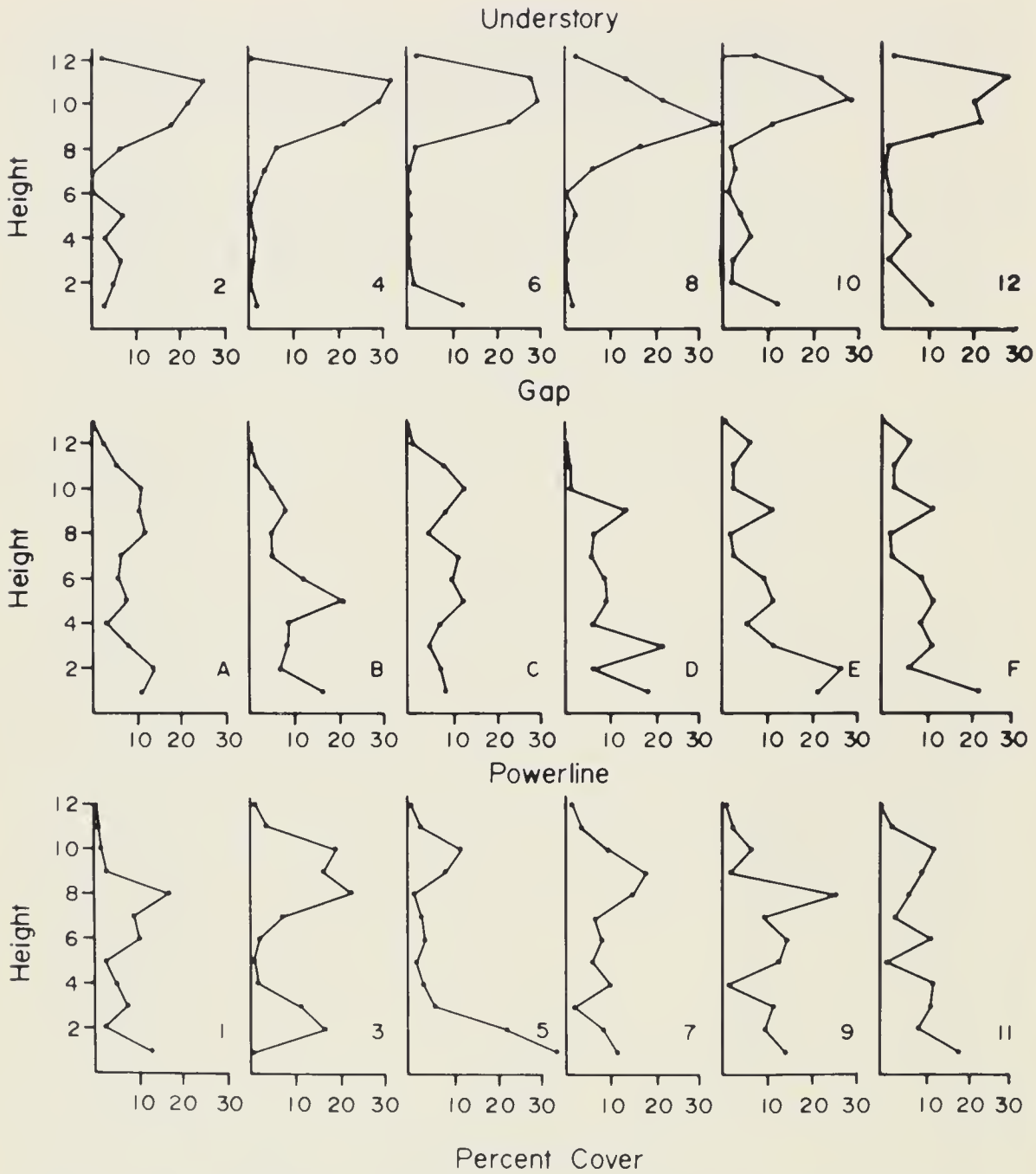

FIG. 2. Foliage height profiles for forest understory (upper), treefall gap (center), and powerline opening (lower) nets. Percent cover represents the percent of vegetation touches in a given height interval. N = 156 sample points per net. Height intervals are in meters (1 = 0–0.25, 2 = 0.25–0.50, 3 = 0.50–0.75, 4 = 0.75–1.0, 5 = 1.0–1.5, 6 = 1.5–2.0, 7 = 2–3, 8 = 3–5, 9 = 5–10, 10 = 10–15, 11 = 15–20, 12 = 20–25).

capture rates differed among the habitats, the total number of species captured in each habitat was similar (13 in powerline, 10 in gaps, 11 in forest); however, the average number of species captured per netting session differed among the habitats. This average was 4.7 species (range = 2–7) in the powerline nets, significantly greater (Mann Whitney $U = 252.5$,

$P < 0.025$) than the mean of 3.3 (range = 2–6) in the gaps, but it did not differ from the mean of 2.4 (range = 0–7) in the forest. Thus the powerline nets captured the largest number of individuals and the highest average number of species per netting session.

Using a Friedman rank sums test we found that six species (Bananaquit, Puerto Rican Tody, Ruddy Quail-Dove, Green Mango, Black-throated Blue Warbler, Puerto Rican Bullfinch) were captured more frequently in one habitat of a pair, providing evidence for habitat preference. Assuming random processes, how many species would be expected to show at least one difference among the three habitat pairs? At the 5% level of significance with three habitats, a minimum of three days in which a given species was captured is required: of the 12 species with three or more capture days, only 0.6 species (12 species × 0.05) would be expected to show differences among habitats based only on random processes. A comparison of this expected number of species (0.6) with the observed number of species with at least one significant difference among habitat pairs (6) indicates that selection among the habitats occurred far more often than expected by chance.

Treefall gaps.—No species was captured exclusively in treefall gaps. Four species, however (Bananaquit, Puerto Rican Tody, Black-throated Blue Warbler, Puerto Rican Bullfinch) were more frequently captured in gaps than in forest.

Powerline opening.—Three species (Bananaquit, Puerto Rican Tody, Green Mango) were captured more frequently in the powerline nets than in the nearby forest. Also, two of these species (Bananaquit, Green Mango) and the Ruddy Quail-Dove were captured more often along the powerline than in gaps, while three species (Puerto Rican Tody, Black-throated Blue Warbler, Puerto Rican Bullfinch) were captured in both habitats with similar frequency. One species, the Green Mango, was captured exclusively in the powerline nets.

Forest understory.—No species was found exclusively in the forest, and none had a higher capture rate in the forest. The quail-dove, however, had an unusual distribution in which the captures in the powerline and forest nets were very similar, but the 19 forest understory captures were significantly greater than the 8 gap captures.

Stream nets.—The presence of a stream (with or without water) had a significant effect on the total number of captures in both the powerline and gap nets (3 and B), but not in the forest (net 8). The powerline net placed across the small temporary stream captured 136 individuals or 45.5% of all powerline captures. This was significantly more ($\chi^2 = 288.49$, $P < 0.005$) than expected (16.7%) from equivalent captures among all 6 powerline nets. The 37 captures (24.8% of all gap net captures) from the

TABLE 2

MEAN AND STANDARD DEVIATION OF SIMILARITY INDEXES FOR PAIRS OF NETS WITH COMPARISONS WITHIN THE SAME HABITAT AND BETWEEN DIFFERENT HABITATS IN EL VERDE

	Powerline	Gap	Understory
Powerline	0.69 ± 0.08		
Gap	0.64 ± 0.11	0.66 ± 0.09	
Understory	0.58 ± 0.11	0.50 ± 0.11	0.65 ± 0.08

gap net across the same temporary stream were also significantly more ($\chi^2 = 10.565$, $P < 0.005$) than expected, assuming equivalent captures in all 6 gap nets. The forest net across the same temporary stream, however, captured only 14 individuals, or 16.8% of forest captures, a value not different from that expected by chance alone ($\chi^2 = 0.00579$, $P > 0.10$).

The total number of species (including migrants) captured in the stream nets in each habitat was approximately 50% of the species captured in all nets in that habitat: 9 species captured in the powerline-stream net represented 56% of all species captured in powerline nets; 5 species from the gap-stream net represented 50% of the species caught in gaps; and 5 species from the forest stream net represented 45% of those captured in the forest. Thus the stream nets in the gap and powerline had higher capture rates than other nets in comparable habitat without streams, and each stream net captured about 50% of all species obtained within the habitat.

Avian assemblages by habitat.—The cumulative species curve combined for gap, powerline, and forest nets plateaued at 10 resident species, with 10 species in the powerline nets, 7 species in the gap nets, and 8 species in the forest. Although the addition of new species to these habitats may still occur, it is likely that it will be slow because all the species previously known from the El Verde forest understory (Recher 1970) were captured.

The mean percentage similarity (PS) for all net-pairs within habitats was significantly different from the mean PS for all net-pairs among habitats (two-tailed Mann-Whitney *U*-test, large sample approximation, $t = 3.712$, $P < 0.001$). Therefore, bird assemblages from net-pairs within the same habitat were demonstrably more similar than assemblages among habitats (Table 2), suggesting that the birds recognized differences among the three habitats.

Several different Bray-Curtis ordinations were made to compare nets in the three habitats. An ordination (Fig. 3A) with all species, including migrants, shows little overlap between gap and forest nets and little over-

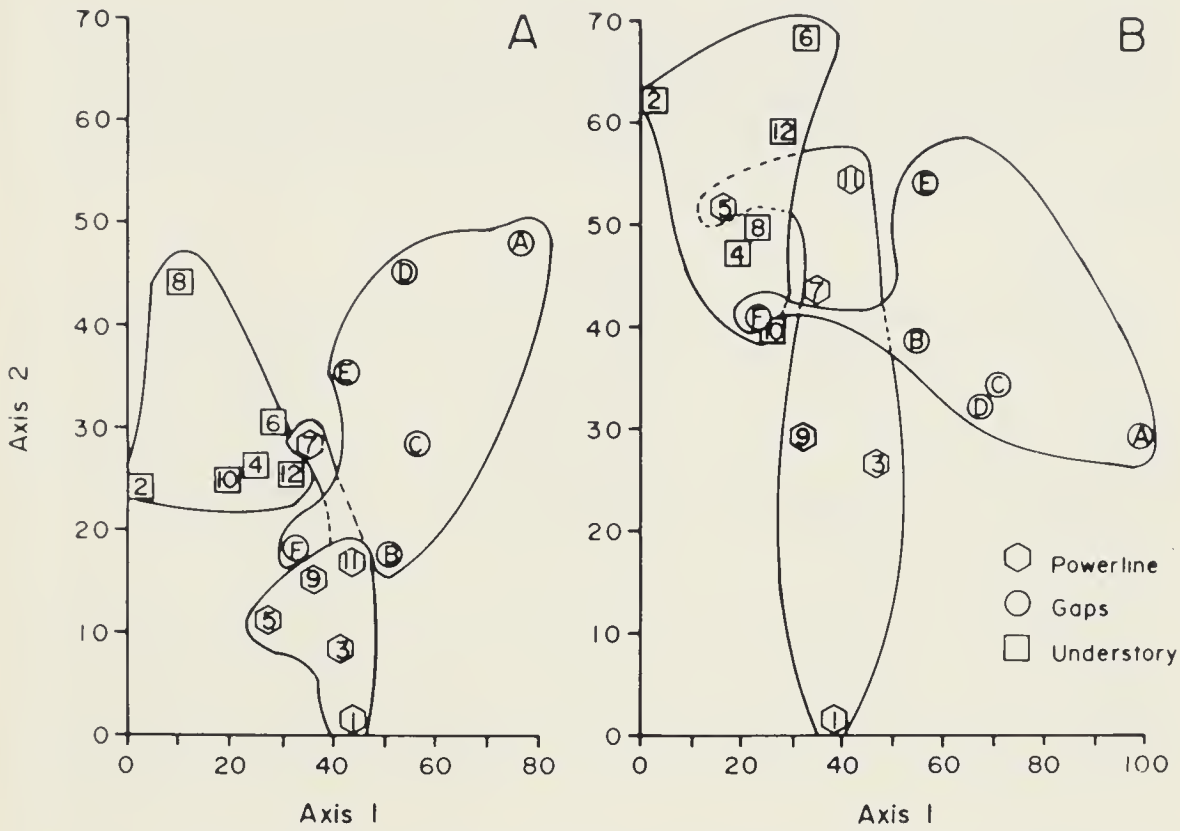

FIG. 3. Ordination of bird captures from forest understory, treefall gaps, and powerline opening nets by the method of Bray and Curtis (1957) for all species (A) and all species except the bananaquit and migrants (B). As shown in Fig. 1, each net is indicated with a number or letter.

lap between forest and powerline nets; however, the overlap of one gap net (F) with the powerline nets suggests more similarity between the two assemblages. Eliminating the migrants (this ordination is not shown) produces better separation of the forest nets from gap and powerline nets, although gap and powerline nets again overlap with net F. Because Bananaquits were the most abundant species (48% of total captures) and were captured significantly more often in powerline nets, they may influence the ordination of all other species. We eliminated this effect by running Bray-Curtis ordinations on a percentage similarity matrix calculated without Bananaquits (see Schemske and Brokaw 1981). The results of these ordinations are similar, suggesting a separation of gap and forest nets, but with some overlap of gap and powerline nets and powerline and forest nets (Fig. 3B).

From the ordinations it is difficult to determine if the presence of running water under a net affected the assemblage of birds captured. For instance, stream nets in the gap (B) and powerline (3) are as similar to each other as to the others in corresponding habitat (Fig. 3A); however,

the forest stream net (8) was very different from these nets as well as the other forest nets. When Bananaquits and migrants are eliminated from the ordination (Fig. 3B) the assemblages of birds captured in stream nets (3, 8, C) are similar to each other and to others in the corresponding habitat.

DISCUSSION

Although treefall gaps in the tabonuco forest may be too small ($\bar{x}$ = 117 m^2 vs 130 m^2 in Panama; Schemske and Brokaw 1981) and rare to support gap specialist species, certain species may spend a comparatively large amount of time in gaps. No species was unique to gaps. With the exception of the mango and bullfinch most of the species were found in all three habitats, although frequently at different abundance levels. All species with higher capture rates in gaps than in surrounding forest understory (Bananaquit, tody, bullfinch, Black-throated Blue Warbler) were also found in the canopy; the higher capture rates of bullfinches and Black-throated Blue Warblers in the gaps may be attributed to their tendency to follow the canopy down into gaps, as has been found for some species in Costa Rican rainforests (Stiles 1983). In some instances, Bananaquits and todies may be following the contour of the canopy in the reverse direction out of the gap into the canopy. Thus, it is the higher abundance of these occasional canopy species that produces the appearance of a gap assemblage different from that of the surrounding tabonuco forest understory. This contrasts with the studies of Schemske and Brokaw (1981) in lowland forest in Panama, where they concluded that differences between gap and forest understory assemblages reflected true habitat preferences of understory birds, rather than a tendency for birds to follow the canopy into gaps.

While the relative abundance of canopy and understory species may affect the composition of the assemblage of species in each understory habitat, the number of resident species from the canopy, understory, or both height zones is nearly identical in each of the three habitats (Table 3). Adding migrants to this analysis substantially increases the number of canopy species in the powerline opening (7 species, 44% of all powerline species) and treefall gap (6, 55%), but not the forest understory (2, 18%). This is because migrants are primarly leaf-gleaning insectivores foraging on sunlit foliage of its height above the ground. The only exception to this was the Louisiana Waterthrush, found in the understory, and usually near streams.

Our findings differ from those of Schemske and Brokaw (1981), who found that although the numbers of individuals captured in gaps and nearby understory were similar, more species were captured in gaps. They attrib-

TABLE 3

SPECIES CAPTURED IN THE THREE HABITATS AND THEIR DISTRIBUTION IN THE FOREST CANOPY OR UNDERSTORY (FOR EACH HABITAT, THE SPECIES ARE SEPARATED INTO RESIDENT SPECIES ONLY AND ALL SPECIES, INCLUDING MIGRANTS)

	Foraging height[a]		
Habitat	Canopy only	Understory only	Canopy and understory
Powerline			
Residents only	2 (20)[b]	4 (40)	4 (40)
All species	7 (44)	5 (31)	4 (25)
Treefall			
Residents only	2 (29)	3 (42)	2 (29)
All species	6 (55)	3 (27)	2 (18)
Forest			
Residents only	1 (13)	4 (50)	3 (37)
All species	2 (20)	4 (40)	4 (40)

[a] Classification of the foraging zone for El Verde birds is based on observations of Waide in Reagan et al. (1982), and Wunderle (unpubl. data).
[b] Percentage of row total.

uted the higher number of species in gaps to the more heterogeneous "edge" habitat of the gap which provides a diversity of foraging opportunities (Terborgh 1977), and to greater foliage density and its higher productivity (Halle et al. 1978) at net height in the gaps rather than high in the canopy (Karr and Roth 1971, Willson 1974).

It is possible that an "edge effect" influenced captures in the forest nets, which were located 10 m from the powerline opening. To examine this possibility we compared our results with those of Waide (in Reagan 1982) who sampled understory birds for 3–4 days using 10–11 nets at three sites in old undisturbed forest at El Verde. Overall, our forest capture rates were 0.055 captures/net (range = 0–0.12 net/h) similar to his value of 0.063 (range = 0.04–0.09 net/h). Comparing the total captures for the 8 most common species, we did find a significant difference between our forest sites and those of Waide (row × column test of independence, $G = 29.27$, $P < 0.005$). However, our higher Bananaquit captures account for this difference, because analysis without Bananaquits indicates no significant difference for the remaining seven species ($G = 8.39$, $P > 0.1$). Thus, our high Bananaquit captures in the forest may have resulted from an edge effect. As the edge effect was not apparent for the other forest species, the ordination without Bananaquits (Fig. 3B) probably best illustrates the forest understory assemblage.

In the tabonuco forest, the gap assemblage appears to be a subset of the assemblage of larger forest openings, represented here by the powerline opening. The mean paired similarity index for gap and powerline was highest of all habitat pairs (Table 2), and when species are ranked by abundance in the gaps and powerline opening, the sequence is the same for the first four species (Bananaquit, tody, emerald hummingbird, quail-dove). Thus the gap assemblage is a subset of the powerline opening (they share 10 species). Comparison of the powerline opening assemblage with even larger second growth openings of similar foliage profile suggests that the abundance of canopy dwelling species, such as the Red-legged Thrush, Pearly-eyed Thrasher, Puerto Rican Tanager, Puerto Rican Lizard-Cuckoo (*Saurothera vieilloti*), Blue-hooded Euphonia (*Euphonia musica*), and Stripe-headed Tanager (*Spindalis zena*) increases with second growth patch size (Wunderle, unpubl. data).

The size of our second growth patches (gaps and powerline opening) was not great enough to discourage forest understory species, which regularly wandered into both gaps and the powerline opening. Only one species, the Ruddy Quail-Dove, can be considered to be primarily restricted to the forest understory in Puerto Rico (Raffaele 1983). Yet this species showed an equal number of captures in the forest and powerline nets and significantly fewer captures in the gaps. Although the distribution of food supply may partially explain this distribution, other factors such as patch size and geometry and the presence of thick understory vegetation may be important.

The distribution of individual species might best be explained in terms of food distribution, which is probably related to vegetation. For those species gleaning insects from the foliage (todies, Bananaquits, Black-throated Blue Warblers, and other warbler species) the gap and powerline opening had the highest density of foraging substrate at net level, and thus more captures of canopy species than in the forest understory nets. Another foliage gleaner, the Black-whiskered Vireo, was captured in forest understory nets only during early April, at a time when vireo territories were being set-up. Similarly, nectarivore distribution can be directly related to flower distribution. For example, the Puerto Rican Emerald was found in all habitats, as were the flowers with short corollas (e.g., *Palicourea crocea*) from which they fed; the Green Mango, which fed exclusively from *Heliconia* flowers, was found only in the powerline opening, the only location of this food source—and the only understory habitat with long-tubed flowers. Mango populations fluctuate with the availability of long-tubed flowers (Kodric-Brown et al. 1984) and will move into any habitat where these flowers are available.

During this study, the rate of understory fruit production was low, although it appeared to be highest in the forest openings, as found in temperate forests (Thompson and Willson 1978) and lowland tropical forest in Costa Rica (Levey, pers. comm.). Thus, higher concentrations of fruit-eating birds in gaps may be a direct result of higher concentrations of fruiting plants in gaps (Willson et al. 1982; Blake and Hoppes 1986; Martin and Karr, in press). Quail-doves are known to congregate under fruiting canopy trees such as *Dacryodes excelsa* and *Sloanea berteriana* (Recher 1970), which are found along the powerline and near the forest understory nets, but are absent along the treefall gaps; this may contribute to their unusual distribution in this study. Similarly, the frugivorous bullfinch was most commonly encountered in treefall gaps, where it fed on the fruits of *Urera baccifera.* This plant was common in gaps, less common in the powerline opening, and absent from forest understory. Fruit abundance in gaps, however, was probably insufficient to attract other canopy frugivores such as the Stripe-headed Tanager, Puerto Rican Tanager, and Blue-hooded Euphonia to the study area.

Karr and Freemark (1983) found that microclimate factors such as moisture gradients influenced bird distributions in tropical forest undergrowth in a complex manner, varying in both space and time. While they did not have food supply data, their data suggested that birds might track microclimatic variables for physiological reasons. In El Verde, running water may attract birds within the more open habitats. Even when water was not present in the temporary streams, the stream nets in the gap and powerline opening still had high capture rates. In fact, the highest seasonal capture rates occurred in the powerline stream net during April when water was not present. It is possible that many canopy species were coming down into gaps in search of water or at least more humid microclimates. Whether food (insects) is more abundant near temporary streams is unknown. Whatever the cause, the presence of a temporary stream appears to make forest openings even more attractive to birds in the tabonuco forest.

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AGGRESSIVE BEHAVIOR OF WINTERING DIVING DUCKS (AYTHYINI)

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ABSTRACT.—Intraspecific aggression, behavioral dominance, and the influence of behavioral dominance on habitat use by the sexes was studied in free-ranging flocks of Canvasbacks (*Aythya valisineria*), Redheads (*A. americana*), Ring-necked Ducks (*A. collaris*), and Lesser Scaup (*A. affinis*) that overwintered in coastal South Carolina. During three field seasons 4316 focal individuals were observed for 5 min each. In Canvasbacks, aggression was more frequent and was more intense than in the other three species. Males of each species dominated females in aggressive encounters that occurred primarily while foraging. In Canvasbacks there was a partial segregation of male and female foraging areas where food resources were distributed irregularly, with greater proportions of males inhabiting the higher quality food areas. *Received 12 Apr. 1985, accepted 15 July 1986.*

Aggressive behavior in animals is a mechanism by which individuals compete for essential, and often limited, resources (e.g., mates, food). Because of aggressive behavior there is frequently an unequal disposition of resources, with dominant individuals having priority of access (Brown 1975, Gauthreaux 1978). Moreover, some researchers indicate that dominant individuals have greater survival probabilities than subordinates (e.g., Smith 1976).

In birds, aggressive behavior is a common phenomenon associated with the reproductive period when males establish territories and compete for mates. Lack (1954) and Fretwell (1972), however, have suggested that, in terms of survival, the nonbreeding period is the more critical portion of the annual cycle. Lack (1966) further suggested that many bird populations are regulated by food supply during the nonbreeding period. In most bird species, a postbreeding tendency to form flocks generates a situation in which aggression is common (e.g., Marler 1971, Jenkins et al. 1975, Patterson 1977). Oftentimes this aggression involves asymmetric contests where males dominate females in competition for food (Brown 1963, Sayler and Afton 1981, Grubb 1982), although the opposite sometimes occurs (e.g., Thompson 1960, Samson 1977). In waterfowl, behavioral dominance has been studied in dabbling ducks (e.g., Paulus 1983, Hepp and Hair 1984), but is poorly understood in diving ducks.

Here, I (1) compare aspects of wintering intraspecific aggression and behavioral dominance in four species of coexisting diving ducks, Canvasbacks (*Aythya valisineria*), Redheads (*A. americana*), Ring-necked

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Ducks (*A. collaris*), and Lesser Scaup (*A. affinis*); and (2) evaluate the effect of behavioral dominance on local habitat use by males and females of each species.

STUDY AREA

I studied free-ranging diving ducks on four coastal manmade impoundments near Georgetown, Georgetown County, South Carolina. The four impoundments ranged from 7.75 to 12.85 ha in size and from 0.50 to 1.50 m in depth. The ponds supported approximately 3500 diving ducks daily from early November to March during 1975, 1976, and 1977. Canvasbacks and Ring-necked Ducks fed on banana water-lily (*Nymphaea mexicana*) tubers in the three freshwater impoundments. All four species fed on muskgrass (*Chara* spp.) and widgeon grass (*Ruppia maritima*) in the one brackish pond.

METHODS

Behavioral sampling.—Diving ducks were observed with 8.5× binoculars, or a 15–60× spotting scope, either from permanent blinds or a vehicle. The behavior of each species was recorded daily during four 40-min intervals spaced 3 h apart. Behavioral data were collected in 4-day cycles throughout each field season, with the 40-min intervals beginning 30 min later each day. Shifting the observation intervals assured that data collected were not biased toward a particular portion of the day. I attempted to study each of the four species every day, but Redheads and Lesser Scaup were frequently absent from the impoundments; species were sampled in a random sequence.

The 40-min observation intervals were partitioned into eight sample periods of 5-min each in which individual birds of a single species were followed continuously. When feasible, equal numbers of males and females were observed within each 40-min interval. Beginning each 5-min sample period, a focal individual was selected from the flock by directing binoculars, or a spotting scope, toward the flock and selecting the individual nearest the center of the field. This bird was the focal individual for the 5-min period, and each behavioral event performed by the bird was recorded in sequence (see Altmann 1974). In agonistic encounters (Scott and Fredericson 1951), the initiator, winner, and loser of the encounter were tabulated.

I defined an aggressive display as any behavioral act performed by one individual that caused the displacement of a second individual. An "intention movement" involved a jab with the bill or a slight movement by one bird toward another bird that was less than 1 m away. A "chase" occurred when one bird paddled rapidly across the water, with its head thrust forward and its bill slightly opened in pursuit of a retreating bird. "Fighting" involved exchanges of biting and striking with the wings. A bird was considered supplanted in an aggressive encounter when it retreated from another individual as a result of a threatening posture or overt activity (e.g., chase). Further descriptions of aggressive displays and fighting are in Alexander (1980a).

Sex and age determination.—Juvenile Aythyini resemble adults by late fall or early winter, and cannot be separated visually in the field. To assess age-related dominance in these species, birds were bait-trapped, aged according to a combination of cloacal characteristics (Hochbaum 1942) and plumage development (Carney 1964), and color-marked with patagial streamers.

Analytical procedures.—The intensity of aggression between wintering diving ducks was assessed by ranking the agonistic encounters on an ordinal scale from levels 1 to 4. Encounters were recorded as level 1 when the presence of one individual supplanted another, as level

2 when one individual supplanted another by an intention movement (e.g., bill thrust), as level 3 when one individual chased another, and as level 4 when two individuals were engaged in a fight (e.g., exchanges of biting and striking with the wings).

Intraspecific sex differences in dominance between unmarked individuals were evaluated by chi-square tests, and dominance matrices (Brown 1975) were used to establish a sex- and age-hierarchy between marked individuals within species.

Once I established intraspecific dominance relationships, I examined the effect of intersexual dominance on flock structure (i.e., male-female encounters more or less frequent than expected by chance). The distribution of intraspecific aggressive encounters between the sexes was analyzed by the goodness of fit to a theoretical distribution with a chi-square test. The existing sex ratio of each species (Hailman 1975) and focal bird sex ratio were considered in calculating the theoretical distribution of encounters. Sex ratio counts were made in early morning while birds were flocked in open water. The sex ratio of each species did undergo some temporal variation on individual ponds, but a decrease in birds on one pond was typically followed by an increase on a nearby pond. Therefore, an average sex ratio was calculated over all ponds. Often, when a population sex ratio has been determined, the proportions of males and females are used to compute an expected distribution of aggressive encounters (e.g., Hepp and Hair 1984). In focal individual sampling, these expected values are biased if the proportions of focal males and females are not also included in the computation of expected values. I calculated expected values for each interaction as follows:

(1) Male-Male = $P_{fm} \times P_{mp} \times TI$
(2) Male-Female = $P_{fm} \times P_{fp} \times TI + P_{ff} \times P_{mp} \times TI$
(3) Female-Female = $P_{ff} \times P_{fp} \times TI$

In the previous equations, P_{fm} = proportion males in focal sample, P_{mp} = proportion males on ponds, TI = total aggressive interactions, P_{fp} = proportion females on ponds and P_{ff} = proportion females in focal sample.

If males and females within species used impoundments independently, the distribution of the sexes within a given pond should occur at random. As I selected focal birds, I also recorded the sex of the nearest conspecific to the focal individuals on each pond. The goodness of fit of male-male, male-female, and female-female associations to a theoretical distribution was tested by the chi-square statistic (see Ketterson 1979). Calculation of expected values included sex ratios and focal bird ratios as above.

Vegetation sampling.—Three impoundments on the study area supported stands of banana water-lily. Aerial photographs indicated that two ponds had uniform distributions of the plant, but at one pond (Middleton) water-lilies had a patchy distribution. On this pond some patches of water-lily leaves covered approximately 100% of the surface area, while in other patches only about 50% of the surface was covered. Bottom sampling for banana water-lily tubers was conducted at 3 m intervals along parallel transects through two contiguous patches near my observation blind. Hereafter, these patches are referred to as areas *a* (100% leaves/m^2) and *b* (50% leaves/m^2). Bottom samples were collected with a sharpened core sampler that extended 20.3 cm into the substrate. Sampling was conducted in October 1978 to estimate the banana water-lily tuber crops in the two areas before birds arrived. In March 1979 sampling was conducted again to document any seasonal decline of tuber crops within the two areas.

RESULTS

Canvasback aggression.—Intraspecific agonistic behavior occurred significantly more often in Canvasbacks than in the other three species (Table

TABLE 1
MEAN NUMBER ± SD OF INTRASPECIFIC AGGRESSIVE INTERACTIONS PER 5-MIN SAMPLE PERIOD IN WINTERING DIVING DUCKS

	Canvasback	Redhead	Ring-necked Duck	Lesser Scaup
Mean ± SD	1.02 ± 1.7[a]	0.47 ± 1.04[b]	0.55 ± 1.18[b]	0.58 ± 1.36[b]
Number of sample periods	1639	452	1441	784

[a] One-way ANOVA ($F = 42.90$, $P < 0.001$). Means not followed by the same letter are significantly different using a Duncan's multiple range test ($P < 0.05$).

1). Moreover, male Canvasbacks initiated 837 intraspecific aggressive encounters during 817 sample periods, while females initiated 495 encounters in 822 sample periods, a difference that was highly significant ($t = 3.24$, $P < 0.001$). In six encounters I could not determine the initiator of the interaction. Of 1338 encounters, 30% involved chasing and fighting. Thirty-one percent of male-male and male-female encounters were at levels 3 and 4, while 26% of female-female encounters were at these levels.

Aggressive encounters between male and female Canvasbacks occurred at a rate of 0.08 interactions/min. A total of 634 aggressive encounters between unmarked males and females was observed, with males winning 416 encounters and females winning 218 ($\chi^2 = 61.8$, df = 1, $P < 0.001$). Male Canvasbacks initiated significantly more intersexual encounters than did females ($\chi^2 = 10.6$, df = 1, $P < 0.005$).

The dominance relationships among sex- and age-classes of Canvasbacks were determined from interactions among 25–40 of 86 marked birds. Adult male Canvasbacks were dominant, followed by juvenile males, adult females, and juvenile females (Table 2). This dominance structure closely parallels differences in body size of the respective sex- and age-classes in the species (see Alexander 1980b for morphological measurements on all four species).

Unmarked Canvasbacks were involved in 1338 intraspecific aggressive encounters. Male-male encounters occurred more often than expected, while female-female encounters occurred less often than expected (Table 3). Similarly, male-male associations were higher than expected and female-female were lower (Table 4). The similarity between these data could suggest an explanation for high male-male and low female-female aggressive encounters based upon frequency of association; however, a χ^2 test for heterogeneity indicated that aggressive interactions in Canvasbacks were not due to proximity alone ($\chi^2 = 14.5$, df = 2, $P < 0.001$).

During this study greater proportions of male Canvasbacks were ob-

TABLE 2

INTRASPECIFIC DOMINANCE RELATIONSHIPS FOR SEX- AND AGE-CLASSES OF WINTERING DIVING DUCKS

Species[a]	Winner	Loser: Adult male	Loser: Juvenile male	Loser: Adult female	Loser: Juvenile female	% wins
Canvasback	Adult male	—	35	71	29	98
	Juvenile male	2	—	27	9	43
	Adult female	1	15	—	30	32
	Juvenile female	0	1	0	—	2
Ring-necked Duck	Adult male	—	40	7	1	100
	Juvenile male	0	—	2	13	27
	Adult female	0	0	—	3	25
	Juvenile female	0	0	0	—	0
Lesser Scaup	Adult male	—	18	28	18	99
	Juvenile male	0	—	5	11	46
	Adult female	1	1	—	11	28
	Juvenile female	0	0	0	—	0

[a] Redheads were deleted from this table because of insufficient data.

served diving in the dense patches of banana water-lily at Middleton Pond. By comparing the Canvasback sex ratio on the pond over a two year period to the sex ratio in densely vegetated area *a*, a pattern of partial sexual segregation while foraging was detected. In addition, the proportion of males using area *a* rose from 38% in November to 86% in January (Table 5). The prevalence of male Canvasbacks in area *a* was likely a result of better food resources there. The bottom samples of banana water-lily tubers from area *a* (100% leaves/m^2) and area *b* (50% leaves/m^2) of Middleton Pond were markedly different. In October 1978 area *a* had whole tubers that were significantly heavier than in area *b* ($t = 2.24$, $P < 0.05$). Moreover, the total weight of whole tubers and fragments cut by the core sampler from area *a* (82.9 g/m^2) was 2.4 times that of area *b* (35.0 g/m^2). When tuber sampling was repeated in March 1979, area *a* had sustained a 50% decline in tubers that was not statistically significant, but area *b* had suffered a highly significant 88% tuber decline ($t = 3.39$, $P < 0.001$). I did not perform similar analyses for the other three species of diving ducks because they did not exhibit sexual differences in foraging patterns on any of the ponds.

Redhead aggression.—Intraspecific agonistic behavior in Redheads was significantly less frequent than in Canvasbacks, but did not differ statistically from Ring-necked Ducks and Lesser Scaup (Table 1). Male Redheads initiated 128 intraspecific aggressive encounters in 239 sample pe-

TABLE 3

χ^2 GOODNESS-OF-FIT TESTS OF THE DISTRIBUTION OF AGGRESSIVE ENCOUNTERS WITHIN SEX CLASSES OF EACH DIVING DUCK SPECIES

Species	Male-male	Male-female	Female-female	χ^2	Probability
Canvasback	485/253[a]	635/668	218/416	308.5	<0.001
Redhead	47/47	104/103	53/55	0.1	>0.050
Ring-necked Duck	232/277	363/364	138/101	20.9	<0.001
Lesser Scaup	163/183	235/228	51/39	6.1	<0.050

[a] Observed frequency of encounters within each category/Expected frequency of encounters within each category (corrected for sex ratio and focal bird differences in each species).

riods, and females initiated 64 encounters in 213 sample periods (t = 0.81, $P > 0.05$). In Redheads, 15% of 204 aggressive encounters involved chasing and fighting. Six percent of male-male encounters were at levels 3 and 4, while 15% of male-female and 23% of female-female encounters were at these levels.

Aggressive encounters between male and female Redheads occurred at a rate of 0.04 interactions/min. A total of 102 intersexual aggressive encounters between unmarked males and females was observed, with males winning 86 encounters and females winning 16 ($\chi^2 = 49.9$, df = 1, $P < 0.001$). Male Redheads initiated significantly more intersexual encounters than did females ($\chi^2 = 20.0$, df = 1, $P < 0.001$).

Unmarked Redheads were involved in 204 intraspecific aggressive encounters. The distribution of male-male, male-female, and female-female encounters was not significantly different ($P > 0.05$) from a random distribution based upon the existing sex ratio and focal bird sex ratio (Table 3). The frequencies of aggressive encounters differed from the frequencies of associations between the sex of the focal individual and that of the nearest conspecific (Table 4). Male-female associations were higher than expected, female-female associations were lower than expected, and male-male associations were about as expected. The distribution of aggressive encounters in Redheads was significantly different from the distribution of associations ($\chi^2 = 8.9$, df = 2, $P < 0.025$).

Ring-necked Duck aggression.—Male Ring-necked Ducks initiated 473 intraspecific aggressive encounters in 730 sample periods, and females initiated 257 encounters in 711 sample periods ($t = 3.97$, $P < 0.001$). Only 14% of 733 interactions involved chasing and fighting. Sixteen percent of male-male encounters, 10% of male-female encounters, and 20% of female-female encounters were at levels 3 and 4.

Aggression between the sexes in Ring-necked Ducks occurred at a rate of 0.06 interactions/min. A total of 366 intersexual aggressive encounters

TABLE 4

χ^2 GOODNESS-OF-FIT TESTS OF THE DISTRIBUTION OF ASSOCIATIONS BETWEEN RANDOMLY SELECTED FOCAL INDIVIDUALS AND THEIR NEAREST CONSPECIFIC NEIGHBOR

Species	Male-male	Male-female	Female-female	χ^2	Probability
Canvasback	334/196[a]	464/519	241/325	124.7	<0.001
Redhead	53/67	206/161	64/96	26.2	<0.001
Ring-necked Duck	288/341	539/461	102/128	26.7	<0.001
Lesser Scaup	164/266	371/331	119/57	111.3	<0.001

[a] Observed frequency of associations within each category/Expected frequency of associations within each category (corrected for sex ratio and focal bird differences in each species).

was observed between unmarked individuals, with males winning 339 encounters and females 27 ($\chi^2 = 266.0$, df = 1, $P < 0.001$). Male Ring-necked Ducks initiated significantly more intersexual encounters than did females ($\chi^2 = 45.8$, df = 1, $P < 0.001$).

Dominance relationships between sex- and age-classes of Ring-necked Ducks were determined from interactions among 40 to 60 of 105 marked individuals. Adult males were dominant, followed by juvenile males, adult females, and juvenile females (Table 2). This dominance order follows the size differences among sex- and age-classes of the species (Alexander 1980b). Only four adult females, however, were trapped and marked during this study, rendering any conclusions about size differences and dominance between adult and juvenile females tentative.

Unmarked Ring-necked Ducks had 733 intraspecific aggressive encounters. Male-male encounters were less frequent than expected, male-female encounters about as expected, and female-female more frequent than expected (Table 3). These data do not coincide with the distribution of associations between the sex of focal individuals and that of the nearest conspecific (Table 4). The frequency of male-male and female-female associations was less than expected, but male-female associations were higher. The distribution of aggressive encounters and distribution of associations in Ring-necked Ducks differed significantly ($\chi^2 = 24.4$, df = 2, $P < 0.001$).

Lesser Scaup aggression.—Male Lesser Scaup initiated 310 intraspecific aggressive encounters in 388 sample periods, while females initiated 138 encounters in 396 sample periods ($t = 0.97$, $P > 0.05$). Of 499 interactions in Lesser Scaup, 12% involved chasing and fighting. Thirteen percent of male-male encounters were at levels 3 and 4, while 12% of male-female encounters and 8% of female-female encounters were at these levels.

Aggressive encounters between Lesser Scaup males and females occurred at a rate of 0.06 interactions/min. A total of 235 aggressive en-

TABLE 5

SEASONAL COMPARISON OF OVERALL CANVASBACK SEX RATIOS ON MIDDLETON POND WITH SEX RATIOS IN AN AREA OF CONCENTRATED FOOD[a]

Period	Overall			Area *a*		
	Males	Females	% males	Males	Females	% males
1 Nov.–15 Nov.	150	213	41	11	18	38
16 Nov.–30 Nov.	370	457	45	75	70	52
1 Dec.–15 Dec.	357	412	46	101	74	58
16 Dec.–31 Dec.	388	230	60	135	50	73
1 Jan.–15 Jan.	577	616	48	158	43	79
16 Jan.–31 Jan.	416	529	44	49	8	86

[a] Data were tabulated during 1976/77 and 1977/78. Because the two years were similar, data were combined (overall heterogeneity $\chi^2 = 1.87$, $P > 0.05$; area *a* heterogeneity $\chi^2 = 2.30$, $P > 0.05$).

counters was tabulated between unmarked males and females, with males winning 205 encounters and females 30 ($\chi^2 = 130.3$, df = 1, $P < 0.001$). In addition, males initiated more intersexual encounters than females ($\chi^2 = 22.7$, df = 1, $P < 0.001$).

Dominance among sex- and age-classes of Lesser Scaup was determined from interactions among 20 to 40 of 115 marked individuals. Adult males were the dominant class followed by juvenile males, adult females, and juvenile females (Table 2). In general the dominance structure followed the size differences among sex- and age-classes (Alexander 1980b).

Unmarked Lesser Scaup had 449 intraspecific aggressive encounters. Male-male encounters were lower than expected, male-female encounters were higher than expected, and female-female encounters were higher than expected (Table 3). These data coincide with the associations found between the sex of the focal individual and that of the nearest conspecific (Table 4). The frequency of male-male associations was lower than expected, but male-female and female-female associations were higher than expected. The distribution of aggressive encounters and distribution of associations in Lesser Scaup were significantly different ($\chi^2 = 23.3$, df = 2, $P < 0.001$).

DISCUSSION

Fretwell (1972) reported that behavioral dominance in winter resulted in the dispersal of birds into an "optimal habitat" in which dominant birds have relatively high survivorship throughout the winter, and a suboptimal "fringe habitat" inhabited by subordinate birds that have relatively low survivorship through the winter. Gauthreaux (1978) reported that important determinants of dominance are sex, age, and size. The

dominance of Canvasback males over females created a partial segregation of foraging areas at Middleton Pond where food resources were irregularly distributed. Males fed more often in areas where banana water-lily tubers were larger, and females fed in less optimal portions of the habitat. Consistently higher proportions of female Canvasbacks were counted swimming into the emergent cattail on this impoundment during foraging, and this area was frequented by predators (e.g., river otters, *Lutra canadensis*; alligators, *Alligator mississippiensis*) during most of the winter. The loss of visual contact with other individuals while foraging in the emergent cattails would make female Canvasbacks more vulnerable to predation. Errington (1946) suggested that individuals forced into marginal habitats by intraspecific competition are often captured by predators. Though little documentation exists on the impact of river otters and alligators on waterfowl, I have observed alligators taking waterfowl (Lesser Scaup, Bufflehead [*Bucephala albeola*], Red-breasted Merganser [*Mergus serrator*]) on three occasions in open water. Indirect evidence that river otters take waterfowl on the study area was derived from observations of duck feathers in feces near otter slides.

The segregation of male and female Canvasbacks, while foraging at Middleton Pond, was not obvious on the other three impoundments where the food resources were regularly distributed; however, the distributions of aggressive interactions and frequency of associations among male-male, male-female and female-female components of the population on all ponds suggested a more frequent association among males. These data seem to indicate that some segregation of the sexes in Canvasbacks takes place on each of the ponds, although it is more subtle in areas where food is regularly distributed, and they support the earlier observations of Olson (1965) concerning an apparent segregation of adult male and female Canvasbacks in the fall.

Redheads, Ring-necked Ducks, and Lesser Scaup did not demonstrate local segregation of the sexes during this study. Moreover, the distribution of aggressive interactions, and the frequency of associations among male-male, male-female, and female-female components of these populations suggested that males and females are found together more often than in Canvasbacks. The close association of the sexes in Redheads, Ring-necked Ducks, and Lesser Scaup may be a result of interspecific competition for food between these three species and the larger Canvasbacks. Male and female Canvasbacks clearly dominated and excluded these species from feeding areas when possible (preliminary data in Alexander and Hair 1979, Alexander 1980b). The three subordinate species seemed to compete more effectively with the larger birds when in pairs or small groups, and this may have produced closer associations among males and females in these species. Their subordination to Canvasbacks may have stimulated more

intense intraspecific competition for food and fighting in Canvasbacks. As well as their competing directly with Canvasbacks for food, the subordinate species might be expected to exploit other less-than-optimal areas in the same habitat, or to migrate to other wintering sites with few or no Canvasbacks. As Redheads and Ring-necked Ducks show some segregation of the sexes by latitude in parts of North America (Alexander 1983), additional research on these species as well as on Lesser Scaup is needed in wintering areas with few Canvasbacks to determine if any sexual segregation occurs there.

Local habitat segregation between wintering male and female Canvasbacks may reduce the rate of aggressive encounters associated with intersexual competition for food. In a variety of nonbreeding woodpecker species, aggression associated with intersexual competition was reduced when males and females segregated feeding niches (Kilham 1965, Ligon 1968, Hogstad 1976, Peters and Grubb 1983) or displayed differences in foraging behavior (Wallace 1974; Hogstad 1977, 1978). If the complete, or partial, segregation of male and female birds at the local or geographic level is a widespread phenomenon during the wintering period, it could be a significant factor in population regulation. Many researchers have demonstrated that the mortality of females exceeds that of males during the nonbreeding period: Phalacrocoracidae (Potts 1969), Anatidae (Geis 1959, Smith 1963, Cooke and Sulzback 1978), Phasianidae (Nelson and Janson 1949), Muscicapidae (Curio 1959), Sturnidae (Davis 1959, Coulson 1960), Icteridae (Darley 1971), and Ploceidae (Ward 1965). If female birds choose suboptimal areas in winter to avoid competition with dominant males, or are forced into these areas, lower quality food or predation could exacerbate the effects of bad weather, increase female mortality, and ultimately skew the population sex ratio in favor of males. If this is so, intersexual competition for food during this period may be an important factor in the regulation of natural populations of these species.

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TIME BUDGET AND INCUBATION BEHAVIOR OF BREEDING WHITE-WINGED SCOTERS

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ABSTRACT.—We studied the behavior and incubation constancy of breeding White-winged Scoters (*Melanitta fusca deglandi*) at Redberry Lake, Saskatchewan, during 1977–1980. Females spent 59.6% of their time feeding during the prelaying period, 61.2% during laying, 60.7% during incubation recesses, and 37% during brood rearing. Prelaying and laying females consistently spent more time feeding than did their mates. Incubation constancy declined from 89.3% of daylight hours during the first third of incubation to 69.3% during the last third. Near the end of incubation, females were off the nest most often between 11:00 and 17:00. White-winged Scoter females probably rely mainly on resources at the nesting area to meet the needs of reproduction. *Received 17 Feb. 1986, accepted 11 July* 1986.

Time-budget studies of breeding dabbling ducks have shown that laying females spend a large amount of time feeding (e.g., Dwyer 1975, Miller 1976, Afton 1979a, Dwyer et al. 1979), and that they spend more time feeding than do males because costs of reproduction are higher in females (King 1973, Ricklefs 1974). Similar information for diving ducks is not available.

During incubation, female ducks must meet their own metabolic needs while simultaneously incubating eggs. Regular incubation recesses suggest a need to feed if feeding is the predominant activity during recesses, whereas more constant incubation implies reliance upon endogenous reserves. Here we describe the time apportionment of breeding White-winged Scoters and evaluate their time budget and nest attentiveness.

STUDY AREA AND METHODS

We studied scoters on Redberry Lake, Saskatchewan, a 6900-ha Federal Bird Sanctuary about 65 km northwest of Saskatoon. Redberry Lake lies in the aspen parkland, and is surrounded by moderately rolling hills. Small grain agriculture and grazing are the predominant land uses. The water is brackish (Rawson and Moore 1944), and the shore and bottom are free of emergent vegetation. All nests were found on islands in the lake.

We captured females on the nest and marked them with nasal saddles (Sugden and Poston 1968). Activity budgets during prelaying, laying, incubation, and brood rearing were estimated from observations of marked females (N = 66) and their unmarked mates. Reproductive status of females was determined by back-dating nests. Behavior was recorded every 60 seconds (1977–78), or every 30 seconds (1979–80). Observations of pairs and females were randomly chosen by site and 2-h interval. Only one marked female and her mate, if present, were observed in sample periods. Observations of females taking incubation recesses

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(i.e., females off the nest) were opportunistic, and individuals were observed for as long as possible. All brood-rearing females had hatched a clutch, and all but two females were with conglomerate broods. Only observations of at least 1 h in duration were included in the analysis. Behavioral activities included: diving, dive pause (time spent on surface between dives), dabbling (feeding with only the head submerged), resting (loafing, sleeping), maintenance (preening, bathing, comfort movements), swimming, alert, interaction (threats, chasing, inciting), courtship or copulation, walking, and flying. Scoters often assumed an alert posture during the dive pause; this behavior was categorized as alert if the head was held high in an alert posture. We recorded a dive pause only if the bird was in a normal resting posture and the bird dove within 30 sec.

We recorded diurnal incubation constancy (i.e., time spent on the nest) of incubating females by focusing time lapse (one frame/sec) Super 8 movie cameras on nests. Data from the day the camera was set up on the nest were not used, and only full days of incubation were included in the analysis. We estimated stage of incubation by candling the eggs (Weller 1956). We obtained daily maximum, minimum, and mean temperatures, and rainfall records from the Meteorological Branch of Environment Canada for the nearby town of Hafford (13 km west of Redberry Lake). Behavioral differences were evaluated statistically with one-way ANOVA's, and correlation measures were estimated using Spearman's rho.

RESULTS

General behavior.—White-winged Scoters did not defend a fixed territory (Brown 1977), but like Velvet Scoters (*M. f. fusca*) (Koskimies and Routamo 1953) maintained a mated-female distance (Conder 1949). Pairs were mobile and often swam more than 1 km away from their original point of observation. We rarely observed marked females more than three times each year.

Prelaying and laying behavior.—Diving (including dive pause) and resting on the water were the most common activities during the prelaying and laying period both for males and females (Table 1). Females spent more time diving ($P < 0.01$), and less time in the dive pause ($P < 0.05$), than did males during prelaying and laying periods. Males spent more time alert ($P < 0.05$) than did females. Females spent more time resting during the prelaying period than did males ($P < 0.05$).

Incubation and brood-rearing behavior.—Total time spent off the nest and recess length (Table 2) were not correlated with maximum, minimum, or mean daily ambient temperatures ($P > 0.40$). Females never left the nest during rainfall (N = 32 bouts of rainfall). Incubation constancy was negatively correlated with stage of incubation ($r = -0.62$, $P < 0.0001$, N = 10 females, 70 days of monitoring) (Table 2). Females were off the nest most frequently between 11:00 and 17:00, corresponding with the warmest part of the day. Mean recess duration was 210 ± 13.1 min [SE] (N = 72, Range = 60–592) and females averaged 223 ± 16.8 (N = 68 days, Range = 0–592) off the nest each day. Females usually took one or two long recesses each day rather than several short recesses (Table 2). During incubation recesses, females spent a greater proportion of their

TABLE 1

DIURNAL TIME-ACTIVITY BUDGET (PERCENT) FOR BREEDING WHITE-WINGED SCOTERS

Behavior	Prelaying		Laying		Incu-bation	Brood rearing
	Male (N = 98)[a]	Female (N = 107)	Male (N = 82)	Female (N = 93)	Female (N = 36)	Female (N = 18)
Diving	35.3	41.8	32.1	43.6	44.8	23.0
Dive pause	21.5	17.2	17.1	17.5	15.9	7.7
Resting	16.4	16.1	12.6	13.0	2.5	10.5
Maintenance	11.4	11.1	10.3	11.7	22.2	13.2
Swimming	8.4	8.3	9.5	9.5	9.3	7.7
Alert	3.7	1.6	16.0	2.4	4.0	23.2
Interaction	1.5	0.9	0.6	0.5	0.1	0.7
Courtship or copulation	0.8	0.6	0.9	0.9	0.0	0.0
Walking	0.0	0.1	0.1	0.1	0.0	0.7
Flying	0.1	0.1	0.0	0.0	0.3	0.0
Dabbling	0.1	0.6	0.0	0.1	0.0	6.1
Out of view	0.6	0.6	0.6	0.5	0.9	0.2

[a] Hours of observation.

time diving, more time in maintenance, and less time resting than during any other reproductive category ($P < 0.05$) (Table 1). During brood rearing, females spent proportionally less time feeding ($P < 0.01$) and more time in alert behavior than at any other time.

DISCUSSION

General behavior.—Defense of the female by the paired male during prelaying and laying may be necessary for females to acquire adequate nutrients for reproduction, as is the case in Common Eiders (*Somateria mollissima*) (Milne 1974, Ashcroft 1976). The mated-female distance behavior allows females to move over large areas while being protected by their mates from harassment by other males. Other studies of scoter feeding ecology and bioenergetics suggest that large feeding areas are required (Brown 1981), making defense of a fixed territory by a breeding female energetically infeasible.

Time-activity allocation.—Differential feeding rates between males and females probably result from their different needs during reproduction. Differences in foraging rates between sexes have been reported for other ducks (see Drobney and Fredrickson 1979, Afton 1979a). Male scoters may not require as much feeding time because their energy and nutrient needs are lower than those of females during reproduction (Brown 1981).

Incubation behavior.—Although nests were not monitored during the night, females were assumed to be incubating because they were always recorded on the nest at dawn or dusk and because marked incubating

TABLE 2
WHITE-WINGED SCOTER NEST ATTENTIVENESS PARTITIONED BY TIME OF DAY AND STAGE OF INCUBATION ON REDBERRY LAKE, SASKATCHEWAN, 1977–1980

Category	Day of incubation		
	1–9	10–18	19–hatch
Mean % time on nest between:			
05:01–11:00	94.9	87.2	82.3
11:01–17:00	79.4	71.0	47.9
17:01–dark	93.7	84.9	79.1
Mean % time on nest during daylight hours	89.3	81.0	69.3
Recesses/day	0.8	1.1	1.3
Mean time off nest (min)/day	116	207	328
Number of days sampled	17	28	25
Number of females sampled	6	9	8

females were never observed elsewhere on the lake during the early evening or morning. In previous studies at Jessie Lake, Alberta (Brown 1977), females consistently returned to their nests before dusk and were present at dawn. As incubation progressed, female scoters spent more of the day off the nest (Table 2).

Mean recess duration (210 min) was much greater than that reported for the Mallard (*Anas platyrhynchos*) (24 min, Caldwell and Cornwell 1975), Maccoa Duck (*Oxyura maccoa*) (35 min, Siegfried et al. 1976), American Black Ducks (*Anas rubripes*) nesting near water (82 min, Ringelman et al. 1982), and Northern Shovelers (*A. clypeata*) (94 min, Afton 1979b), but similar to American Black Ducks nesting at upland sites (183 min, Ringelman et al. 1982). Scoters spent more time (223 min) off the nest each day than did Mallards (78 min, Caldwell and Cornwell 1975), marsh-nesting American Black Ducks (201 min, calculated from Ringelman et al. 1982), and Northern Shovelers (221 min, Afton 1979a, b), but less than Blue-winged Teal (*A. discors*) (289 min, Miller 1976), and upland nesting American Black Ducks (310 min, calculated from Ringelman et al. 1982).

Afton (1979a) compared the incubation behavior of Northern Shovelers to that of several other anatids, and suggested that smaller female anatids rely more on breeding-ground resources than larger anatids because of their inability to store a large endogenous reserve. Scoters apparently do not fit this pattern (see also Ringelman et al. 1982). Species that rely on endogenous reserves to meet metabolic needs during incubation have higher rates of nest attentiveness than do species that must feed to meet their needs (Afton 1979a, 1980). Incubation constancy is probably more

closely linked with the strategy of energy allocation employed by a species than with body size, although body size is a good indicator of the energy strategy of the species.

The incubation behavior of female scoters might also be influenced by the long distances ($\bar{x}$ = 96 m) nests are from water (Brown and Brown 1981). The energy required to rewarm eggs following an incubation recess (per minute of recess) is lower for females that take long recesses; a single recess is the most efficient incubation rhythm (Drent 1973).

Several characteristics may allow scoters to spend less time on the nest as incubation progresses. They nest during the warmest part of the summer, select dense nest cover, and line their nest with down (Brown 1977, Brown and Brown 1981). Also, embryonic heat production may increase during the later stages of incubation as found in other species (Drent 1970, White and Kinney 1974).

Four reproductive strategies have been identified in temperate and arctic nesting anatids (Owen and Reinecke 1979). These strategies represent points on a continuum related to (1) reliance on either stored or environmental resources to provide most of the energy used for reproduction, and (2) the location from which endogenous reserves are accumulated, either on or away from the breeding areas. Carcass composition studies of breeding female scoters have shown that lipid content changes little during laying, and that it begins to decline only after the onset of incubation (Brown 1981). This finding, combined with the high proportion of time females fed (i.e., dove) during the prelaying and laying periods, and their declining incubation constancy as incubation progresses, suggests that they rely mainly on resources on the breeding ground to meet most of their needs for reproduction.

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ASSOCIATION OF MALE AND FEMALE AMERICAN ROBINS (*TURDUS MIGRATORIUS*) DURING THE BREEDING SEASON: PATERNITY ASSURANCE BY SEXUAL ACCESS OR MATE-GUARDING

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Abstract.—Male American Robins (*Turdus migratorius*) behave in ways consistent with the protection of paternity hypothesis. During nest building and egg laying when females are fertilizable, males are with females significantly more often than they are during incubation when females are assumed to be nonfertilizable. Males are significantly closer to females and follow them significantly more often during fertilizable than nonfertilizable periods. Our data suggest that neither reduction in the risk of predation or other direct advantages to females select for the observed variation in the behavior of males. We therefore conclude that male behavior is a probable result of selective advantage gained through paternity assurance, though not necessarily through mate-guarding. *Received 15 Jan. 1986, accepted 4 Sept. 1986.*

Sperm competition probably occurs in at least 26 avian families (McKinney et al. 1985); most of the species are sociographically monogamous (Wickler and Seibt 1983), i.e., males and females consort in pairs, confirming the prediction that mixed reproductive strategies among avian males are common (Trivers 1972). When care of offspring is costly to males, selection against males who care for nonlineally related offspring should occur, and behavior consistent with functional interpretations of protection of paternity should arise.

Protection of paternity can be inferred from differential distribution of parental resources to lineal and nonlineal offspring (implying kin recognition) and from other behavior that increases the probability that females produce offspring sired only by a given male. Mate aggression (Barash 1976), differential responsiveness to courtship cues (Erickson and Zenone 1976), and so-called "mate-guarding" or surveillance of females (Lumpkin et al. 1982) all have been interpreted as behavior increasing the probability that offspring are biologically sired by the males performing the behavior.

Functional interpretations of protection of paternity are often based on predictable variation in behavior. For example, if protection of paternity takes the form of male attendance of females, behavior that could vary includes following of females by males, proximity of males to females,

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and interference by males in interactions of females with other males (e.g., Beecher and Beecher 1979, Birkhead 1979, Mumme et al. 1983). Assessment of the existence and function of aggression between females and males, or courtship differences in wild bird populations is dependent on chance observations of rare events or experimental manipulation of rare events (Erickson and Zenone 1976, Gowaty 1981). In contrast, assessment of existence of attendance depends on relatively easily collected behavioral samples of free-ranging individuals.

American Robins (*Turdus migratorius*) are sociographically monogamous, and males and females cooperate in feeding and defense against predators of nestlings and fledglings (Verner and Willson 1969). We asked if males behaved towards females in ways consistent with protection of paternity through attendance. If so, we expected that (1) males would be with fertilizable females more frequently than with nonfertilizable females, (2) males would stay closer to fertilizable females than to nonfertilizable females, and (3) males would follow fertilizable females more than they followed nonfertilizable females. In this paper we document variability in behavior of male robins consistent with these predictions. We conclude, however, that the functional significance of these attendance patterns remains in question.

METHODS

We watched robins on the lawns and gardens of the Cornell University campus primarily in the experimental garden of the Cornell Plantations. Focal individuals were females with whom we could associate a particular nest. Females, associated with 27 nests, are included in these samples. Ten of the focal females were color banded; others were not. Three males that were seen with females were also color banded. We sampled behavior during nest building, egg laying, and incubation stages of the nest cycle at irregular intervals always before 12:00 EST. For the analyses presented here we considered nest building and egg laying stages to represent *fertilizable* periods for females and the incubation stage as a *nonfertilizable* period. Twenty-five observation bouts were conducted during nest building, 10 during egg laying, and 29 during incubation. Observation bouts yielded 31 samples: females from 4 nests were sampled during both periods, 27 were sampled during only one period. Total minutes of observation were 429 for nest building, 237 for egg laying, and 704 for incubation; thus sample time was almost evenly distributed between fertilizable (666 min) and nonfertilizable (704 min) females. Observation bouts were terminated if we lost track of focal females. Observation bouts lasted 19 ± 9 min [SD] for fertilizable periods; and 24 ± 8.4 min during nonfertilizable periods.

We sampled motor patterns in three ways consistent with Mumme et al. (1983): (1) At minute intervals during sample periods (of a maximum 30 min), we recorded on check sheets whether females were within 30 m of other robins and, if so, the sex of the other robin(s). (2) At each minute interval we also recorded the estimated distance apart in meters of focal females and of the individual(s) within 30 m of her. (3) Whenever a focal female or her male "attendant" moved by flying away, we recorded both which individual initiated the movement and whether the other followed within 30 sec.

Sexes of robins were assigned on the basis of hood color and head and nape contrasts (e.g., see Gochfeld and Burger 1983), and behavior. We determined the sex of color-banded individuals by the presence of a brood patch in females or a cloacal protuberance in males. We assumed that unbanded individuals were females if they carried nesting material, built nests, or incubated eggs, activities usually confined to females among robins (Verner and Willson 1969).

Statistical tests are from Sokal and Rohlf (1981) and Siegel (1956); all tests were one-tailed.

RESULTS

Males were seen within 30 m of focal females in 87% of the 31 samples. During fertilizable periods 100% (N = 16) of females were with males (also called "attended by males") during some part of the sample; in contrast, during incubation 73% (N = 15) of females were with males during some part of the sample ($G = 6.444$, df = 1, $P < 0.01$). Similarly, the total time that females were or were not attended by males was associated with fertilizability. Females were attended by males for greater proportions of each sample time during fertilizable periods than during nonfertilizable periods (for arcsin transformed data $t = 3.7828$, df = 29, $P = 0.00035$). The mean percent of each sample during which a female was attended was 77% during fertilizable periods and 28% during nonfertilizable periods.

The mean distance apart for males and females was 6.3 m during fertilizable periods and 9.6 m during the nonfertilizable periods ($t = -1.5198$, df = -25, $P = 0.07$).

Females initiated 74% of all movements and were followed by males 53% of the time. The likelihood that a female was followed by a male was associated with fertilizability ($G = 19.672$, df = 1, $P < 0.001$). Males followed females at least once in 93.7% of samples during fertilizable periods but in only 20% of observations during the nonfertilizable periods. When counts of following of females by males are examined for association with fertilizability, the hypothesis of independence is clearly rejected. During fertilizable periods females were followed by males more often than expected (88 out of 142 female initiated movements), and not followed less than expected (54 out of 142 female initiated movements). During nonfertilizable periods females were followed by males less than expected (8 of 38 female initiated movements) and not followed more than expected (30 of 38 female initiated movements) ($G = 20.9852$, df = 1, $P < 0.001$). When males initiated movements, females followed them at least once during 37.5% of fertilizable periods but only during 6.7% of nonfertilizable periods ($G = 4.6$, df = 1, $P = 0.032$). However, when counts of following of males by females are examined for association with fer-

tilizability, the hypothesis of independence cannot be rejected ($G = 3.2054$, df = 1, $P < 0.10$).

DISCUSSION

The behavior of male robins is associated with fertilizability of females. Predictions of the uncertainty of the paternity hypothesis are met by these data: compared to nonfertilizable females, fertilizable females were attended by males more frequently than were nonfertilizable females, and males followed females more frequently than the reverse.

What evolutionary hypotheses can explain the close attendance and following of females by males and are consistent with these data?

(1) Variation in close affiliation by males of females may be the result of selection for "mate-guarding," defined as behavior by males that inhibits or interrupts sexual advances of other males to females with which the "guarding" male associates. Mate-guarding has been inferred from similar data in a variety of species (e.g., Beecher and Beecher, 1979; Birkhead, 1979, 1982). Our data, however, are inadequate to claim mate-guarding among robins. Roughly a third of the females, but only a tenth of the males we observed were marked individuals. Thus we cannot comment on the duration of the associations we did observe; we do not know if all of the males we watched attending females were bonded to them and thus their mates. Secondly, it seems difficult to differentiate guarding from alternative explanations (see (2) below) for variation in the behavior of males we observed.

(2) Close affiliation of females and males during nest building and egg laying may be the result of selection for the males' opportunities to copulate irrespective of any protection of paternity from competitive sources. This hypothesis predicts that males should affiliate with and follow females only during those times of day when copulations are likely to occur. Because most of our samples were collected before 10:00, we cannot comment further upon this idea. Additional needed data include a frequency distribution of copulations during the day. We observed copulation at all hours of the morning except for the hour after dawn; we do not know if copulations occurred during midday, afternoon, evening, and night. Even with appropriate data on circadian distribution of copulations, variation in attendance patterns attributable to this hypothesis would be difficult to differentiate from variation associated with protection of paternity, an undiscussed difficulty in interpretation of many studies of mate-guarding (e.g., Birkhead 1979, 1982). Ways to differentiate the guarding hypothesis from the copulatory access hypothesis include noting variation in behavior of males with females during a single day. If after copulation

is achieved, males discontinue following and close association with females, the guarding hypothesis would be weakened. Critical evaluation of the existence of mate-guarding also depends on observations of social situations in which more than one male may have access to fertilizable females (e.g., Mumme et al. 1983). Given that the robins we observed were only weakly territorial with as many as 10–12 nests in a few acres, we can claim that more than one male may have had access to a given female. We are unable, however, to offer comparisons of robins under more dispersed, strongly territorial nesting conditions.

(3) Close attendance and following of females by males may be a reflection of the increasing bond concurrent with the pair formation phase of the nesting cycle. This pairbond explanation for close attendance and following predicts that the mechanisms of association will intensify as the breeding cycle continues (Lumpkin et al. 1982). The significant decrease in attendance and following of females by males from fertilizable to nonfertilizable periods allows the rejection of this prediction of the increasing-bond hypothesis.

(4) Close attendance and following of females by males may be the result of selection against predation. If predation has selected for male behavior, i.e., if the risk of predation on females is reduced by the presence of males, males should attend and follow females during nest building and egg laying as well as incubation with about equal intensity, or with greater intensity during incubation when the female and nest are presumably of greater reproductive value to males. Our data do not support this hypothesis. For example, males followed females more during nest building and egg laying and less during incubation rather than the reverse pattern. Reduction in predation risk may contribute some selective advantage; however, reduction in this risk alone cannot account for the observed variation in attendance, following, and proximities to females by males.

(5) Another hypothesis, related to (2) and suggested by consideration of advantages to females in shaping the behavior of males (Lumpkin 1981), is that females gain direct benefits from close attendance of males, e.g., reduction in the probabilities of forced extra-pair copulations or predation. This hypothesis predicts that males initiate movements as frequently as females and that females follow males as often as males follow females. Our data lend little support to the notion that females manipulate the attendance behavior of males, although it should not be overlooked that the frequencies with which females did or did not follow males at least once during a sample is associated with fertilizability. This may mean that females gain benefits such as protection from unwanted copulations with other males or that association may reflect female so-

licitation of copulations. We observed few copulations, and none of these gave evidence of force. Furthermore, females always were able to chase males away from nests when intruder males approached. We therefore suspect that female robins are able to avoid forced copulations and to defend themselves against predators without male help. We are unable to comment further on female "solicitation" because we observed so few copulations.

(6) A final hypothesis states that changes in foraging requirements associated with different periods of the nesting cycle shape attendance and following. While it does seem likely that nutritional requirements for females may vary with nest cycle periods, it seems unlikely that variation in nutritional needs can explain the attendance and following behavior of males unless male robins are less successful than female robins in finding food during early stages of nest cycles.

We conclude that male robins behave in ways consistent with the protection of paternity hypothesis. Based on our observations, we *predict* that male robins engage in a mixed reproductive strategy, cooperating with one female in the care of offspring while taking opportunities to copulate with other females in whose offspring they do not invest. The variation in male attendance behavior suggests that a similar study on a universally marked population of individuals would be profitable.

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GEOGRAPHIC VARIATION IN TESTIS SIZE IN SAVANNAH SPARROWS (*PASSERCULUS SANDWICHENSIS*)

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Abstract.—Body size and testis size are positively correlated among 1165 Savannah Sparrows (*Passerculus sandwichensis*) from 48 localities. Body size accounts for 5–7% of the variation among individuals in testis size, and for about 30% of the variation in average testis size among populations. Testis size and latitude are negatively correlated, and latitude per se better predicts testis size than does a variety of direct measures of the climatic environments at the collecting sites. The testis sizes of males from polygynous populations average larger than those of males from monogamous populations. However, the differences between "polygynous" and "monogamous" males are slight, and males from Halifax and Sable Island, Nova Scotia, where the species is known to be polygynous, have *smaller* testes than predicted. There is no correlation between testis size and the amount or extent of yellow in the superciliary stripe—a measure of plumage brightness. The average testis volume of Savannah Sparrows resident in saltmarshes along the west coast of Mexico and southern California is greater than that from other populations. *Received 22 Jan. 1986, accepted 14 July 1986.*

In birds, there is a pronounced increase in the size of the testes during the breeding season. Histologically, this increase in size occurs primarily as a consequence of the enlargement of the seminiferous tubules, in which sperm are produced (Lofts and Murton 1973). In Great Tits (*Parus major*), resident in Sweden, the testes remain large throughout the mating season even though the size of the Leydig cells (where testosterone is produced) decreases after the period of time during which male territoriality is maximal (Silverin 1978, Röhss and Silverin 1983). Similarly, Wingfield (1984) found that testes of male Song Sparrows (*Melospiza melodia*) are maximally enlarged when females are laying, and hence when they are copulating. The testes of Song Sparrows from New York, where birds are double-brooded, remain maximally large until after the second brood has been laid, even though endocrine activity decreases substantially before the young in the first brood have hatched. Therefore, it is reasonable to assume that the testis size is an approximate reflection of the quantity of sperm produced, and hence of sperm demand, although this has not been shown directly for any bird species.

In primates, males in genera with multimale breeding systems have relatively larger testes than do males in genera with single-male breeding

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systems. In multimale species, several males may copulate with an estrous female, and it appears that sperm competition selects for large testis size (Harcourt et al. 1981). In birds, Cartar (1985) found that among 18 species of sandpipers (Subfamily Calidridinae), males of species with nonmonogamous mating systems generally had larger testes (relative to body mass) than did males of species with monogamous mating systems. In shorebirds the opportunity for males of nonmonogamous species to mate with several females in a season is probably a more important factor than sperm competition in the evolution of testis size (Cartar 1985).

Here, I relate interpopulational variation in testis size within Savannah Sparrows (*Passerculus sandwichensis*) to body size and presumed age, as well as to various aspects of natural history, including differences in breeding biology.

Savannah Sparrows are widespread and abundant North American songbirds. Throughout most of their range, they breed in mesic sedge or grass meadows, hayfields, or pastures. In the southwestern United States and western Mexico, however, they breed in coastal saltmarshes. In contrast to other Savannah Sparrows, which are migratory, these saltmarsh sparrows are resident, although there is some postbreeding wandering (van Rossem 1947). There have been several studies of the natural history of nonsaltmarsh Savannah Sparrows, but little is known about the biology of the saltmarsh birds. Therefore, I shall analyze interpopulational variation in testis size in the nonsaltmarsh and the saltmarsh birds separately.

The mating system of Savannah Sparrows varies from population to population. Stobo and McLaren (1975) and Welsh (1975) found that males are frequently polygynous on Sable Island and near Halifax, Nova Scotia, whereas Weatherhead (1979) and Bédard and Meunier (1983) found them to be monogamous near Churchill, Manitoba, and Isle Verte, Quebec.

I assume that sperm demands are highest in the populations where males are commonly polygynous, where males are selected to be capable of fertilizing two clutches of eggs in relatively less time than in "monogamous" populations, and, on occasion, to do so virtually simultaneously. I predict that this would select for relatively larger testes (greater volume of seminiferous tubules) in such places.

METHODS

I collected samples of Savannah Sparrows from sites throughout North America, including Sable Island and Halifax, Nova Scotia, and Churchill, Manitoba. When possible, I measured the length and width of the largest (almost always the left) testis on each specimen. I made the majority of the measurements, but for some samples others took the measurements. Each specimen was weighed and the skin and skeleton saved and measured (these are in the Royal Ontario Museum, Toronto, Canada); thus I have information about both body and testis size and plumage coloration for each individual.

I used testis volume as a measure of testis size and estimated volumes using the formula for the volume of a prolate spheroid, where volume = $0.52(\text{length})(\text{width})^2$. Because these volumes are log-normally distributed, I used a log transformation of volume to facilitate statistical analyses. Cartar (1985) used testis length as a measure of testis size.

As mentioned above, of the many factors that may affect testis size within a species, seasonal variation in gonadal activity is surely the most important. Here I present data only on "breeding" males, that is, males that, when collected, were apparently on territories during a time of the year when the majority of males were establishing territories, defending territories, or feeding young. In total, I have information on 1433 "breeding" male Savannah Sparrows, but for these analyses not all of these were used. I have omitted samples taken either very early or very late in the breeding season, and discarded small samples, leaving 1020 nonsaltmarsh and 145 saltmarsh birds from 48 different localities. From two localities, Kleinburg, Ontario, and Woodruff, Utah, there are two different samples taken on different dates and in different years (Table 1).

Among the 48 samples from different localities, several, in addition to those from Sable Island and Halifax, are from maritime Canada (Table 1). Because the ecological conditions at these sites are similar to those at Sable Island and Halifax, I assume that males in these populations are similarly selected to be polygynous. While this seems a reasonable assumption, it might not be a correct one. Dixon (1978) did not find polygyny in Savannah Sparrows breeding on Kent Island, New Brunswick, although this was not apparently an aspect of breeding biology that she was especially studying.

For a sample of populations probably selected to be monogamous, I used, in addition to Churchill, Manitoba, 7 other samples from high latitudes, where the breeding season is short; Weatherhead (1979) found that it was the short nesting season that selected for monogamy at Churchill. Additionally, Lein (1968, pers. comm.) and Potter (1972, 1974, pers. comm.), who studied Savannah Sparrows near Saskatoon, Saskatchewan, and Ann Arbor, Michigan, respectively, found that, on their study sites, the sparrows were almost always monogamous. On the basis of these studies, I included 3 samples from the Canadian prairies and one from Wallaceburg, Ontario (close to Ann Arbor) in the monogamous sample (Table 1). Because monogamy is apparently widespread in the species, it is probable that many if not all of the samples in the "unknown mating system" category are composed of generally monogamous males; the selection of these 11 samples for the "monogamous" group is conservative.

In the following analyses, I used the information on each individual when relating testis size to characteristics of individuals (e.g., body size, "age"). Because all of the variables are normal deviates and the variances are homogeneous, I used parametric correlation analyses to assess the significance of relationships between variables, and *t*-tests or ANOVA to assess significance of differences between or among groups. I used regression and correlation analyses to assess the relationship between testis size and the log of weight among individuals. Because there is a significant relationship between testis size and weight (see below), in some analyses I used the residual values of testis volume, regressed against log weight, to "correct" for variation in body size.

In Northern ("Baltimore") Orioles (*Icterus galbula*), males breeding in their first year have smaller testes than do older breeding males (Flood 1980). As in orioles, Bédard and LaPointe (1984) found that the proportion of yearling Savannah Sparrow males that obtained mates was significantly less than the proportion of older males that obtained mates. Therefore, the average sperm demand on yearling males would be less than that for older ones, perhaps leading to (or because of) smaller testis size. I have no direct way to assess the age of the Savannah Sparrows used in this study (they were all at least one year old). However, the brightness of the plumage increases with age in many species. There is little apparent

TABLE 1

SAVANNAH SPARROW TESTIS VOLUMES AND FEMUR LENGTHS

Location	*N*	Femur length[a]	Volume[b]	Latitude[c]
"Polygynous" samples				
Sable Island, Nova Scotia	24	19.0	5.61	44.00
Halifax, Nova Scotia	12	17.7	5.50	44.67
River John, Nova Scotia	31	17.6	5.78	45.84
Parson's Pond, Newfoundland	13	17.7	5.45	50.00
Bedeque, Prince Edward Island	25	17.3	5.56	46.33
St. Andrews, New Brunswick	21	17.4	5.69	45.16
Magdalen Islands, Quebec	28	17.6	5.44	47.50
"Monogamous" samples				
Churchill, Manitoba	28	17.2	5.30	58.84
Gillam, Manitoba	17	17.2	5.28	56.33
Ft. Chimo, Quebec	20	17.5	5.39	58.16
Winisk, Ontario	40	17.3	5.42	55.33
Yellowknife, Northwest Territories	15	16.9	5.15	62.50
Norman Wells, N.W.T.	21	17.0	5.18	65.33
Coppermine, N.W.T.	30	17.1	5.49	67.84
Inuvik, N.W.T.	14	16.8	5.07	68.33
Wallaceburg, Ontario	37	17.3	5.45	42.67
Milk River, Alberta	29	16.9	5.35	49.16
Grande Prairie, Alberta	26	16.9	5.50	55.16
Samples with unknown mating system				
Matane, Quebec	29	17.2	5.59	48.84
Kleinburg, Ontario (16 May)	17	17.1	5.72	43.84
Kleinburg, Ontario (20 May)	25	17.1	5.63	43.84
Sowerby, Ontario	23	17.4	5.51	46.33
Cochrane, Ontario	22	17.4	5.18	47.84
Moosonee, Ontario	44	17.0	5.43	51.33
Attawapiskat, Ontario	35	17.1	5.41	53.00
Portage La Prairie, Manitoba	35	17.1	5.30	50.16
The Pas, Manitoba	20	17.1	5.37	53.84
Owen's Lake, California	18	17.2	5.37	36.50
Brandonville, West Virginia	24	17.2	5.66	39.58
Woodruff, Utah (18 May)	21	17.1	5.36	41.50
Woodruff, Utah (10 June)	24	17.3	5.54	41.50
Elberta, Utah	18	17.0	5.41	40.00
Halleck, Nevada	18	17.1	5.38	40.87
Sheridan, Wyoming	31	17.1	5.51	44.78
Creston, Washington	33	17.0	5.44	47.67
Eureka, California	24	17.4	5.50	40.67
Wasilla, Alaska	26	16.9	5.44	61.16
Fairbanks, Alaska	21	16.7	5.20	65.00
Umnak Island, Alaska	26	18.5	5.68	55.33

TABLE 1
CONTINUED

Location	*N*	Femur length[a]	Volume[b]	Latitude[c]
Port Heiden, Alaska	16	17.6	5.67	56.83
Cold Bay, Alaska	15	18.2	5.74	55.00
Middleton Island, Alaska	25	17.8	5.51	59.50
Saltmarsh samples				
Puerto Peñasco, Sonora	9	17.9	5.50	31.33
Kino, Sonora	21	18.1	5.89	28.84
El Molino, Sinaloa	17	18.3	5.86	24.50
Magdalena Bay, Baja Cal. S.	14	18.2	5.34	24.33
Guerrero Negro, Baja Cal. N.	33	17.7	5.85	28.00
Bahia San Quintin, Baja Cal. N.	20	17.2	5.68	30.33
San Diego, California	19	17.0	5.56	33.33
Morro Bay, California	17	17.1	5.56	35.33

[a] Average (mm).
[b] Log of testis volume (mm^3).
[c] Converted to decimals (i.e., 47°40′ = 47.67).

variation in plumage coloration in Savannah Sparrows, but there is a variable amount of yellow in the superciliary (of both sexes) that might be of some significance in display and that might increase with age. I scored each specimen on a scale of 1 (no yellow) to 5 (extensive and bright yellow). As a possible test of the relationship between age and testis size, I correlated this superciliary score with the log of the testis volume.

To assess patterns of interpopulational variation, I used stepwise multiple regression (SPSSX Subroutine REGRESSION), regressing the log of the average testis size from each site, against seemingly relevant characteristics of the site or the sample, namely: (1) day of collection, (2) latitude, (3) longitude, (4) elevation, (5) average June temperature at a weather station near the site, (6) average femur length of the males at the site (skeletal measurements), (7) log of average mass of the males, and (8) an estimate of the reproductive condition of the females at the time the birds were collected. At each locality I collected females as well as males, and also examined their gonads. The estimate of female reproductive condition was the percentage of these females that were either pre-laying or laying. The percentages were transformed by arcsin to reduce skewness.

I selected these independent variables to reflect geographic variation in both climate and the birds' size. The timing of reproduction varies from locality to locality. For example, judging from the reproductive condition of the females collected, the birds at Owen's Lake, California, on 14 May and those at Moosonee, Ontario, on 12 June were at comparable stages in their nesting cycle. The variables latitude, longitude, elevation, day of collection, percentage of females laying, and June temperatures relate to this interpopulational variation in climate and seasonality. The average femur length and mass reflect body size, and these variables were included to account for geographic variation in body size.

RESULTS AND DISCUSSION

The correlation between date of collection and log testis volume among the 1020 nonsaltmarsh males is $r = -0.08$ ($P < 0.01$), and that between

volume and date for the 145 saltmarsh males is $r = 0.10$ ($P > 0.05$). Thus, less than 1% of the variation in testis size among the birds used in these analyses is explained by differences in the dates of collection.

The correlation between the log body weight and the log testis volume in the total sample is $r = 0.26$ (N = 1157, $P < 0.01$). Within the nonsaltmarsh birds, this correlation is $r = 0.23$ (N = 1011; $P < 0.01$), and within the saltmarsh birds, it is $r = 0.27$ (N = 146; $P < 0.01$). Thus, 5–7% of the variation among individuals in testis volume is explained by variation in body size; this relationship does not appear to differ between saltmarsh and nonsaltmarsh birds.

The correlation between the testis volume and the extent and intensity of the superciliary stripe is $r = -0.02$ (N = 1011; $P > 0.05$).

The average testis volume of the 154 males collected from "polygynous populations" is significantly larger than that of 277 males from "monogamous populations" (5.59 vs 5.36; $t = 5.99$, df = 429, $P < 0.001$). Also, the testis volume of the saltmarsh sparrows is larger than that of the nonsaltmarsh birds (5.66 vs 5.46, $t = 2.66$, df = 1163, $P = 0.01$). Both the polygynous and the saltmarsh birds, however, are larger on average than nonsaltmarsh birds (see femur lengths in Table 1). I regressed log testis volume on log weight to correct for the relationship between testis size and body size, and used the residuals as a measure of testis size that is independent of body size. There is a significant difference between the average residual variation of the 154 polygynous males and the 277 monogamous males (0.015 vs −0.107; $t = 3.07$, $P = 0.002$), and a significant difference between the 146 saltmarsh vs the 1011 nonsaltmarsh birds (0.165 vs −0.023; $t = 6.09$, $P < 0.001$). Thus, the differences in testis size between monogamous and polygynous birds, on the one hand, and nonsaltmarsh and saltmarsh birds, on the other, are significant even when the among-individual variation in size is accounted for.

In the stepwise multiple regression, only two variables, "femur length" and "latitude," were entered (in that order) using a significance criterion of $P < 0.05$. Thus, with the covariation with femur length and latitude accounted for, none of the other measures—log weight, longitude, elevation, June temperature, date of collection, and reproductive condition of females—are significantly correlated with testis volume. Femur length is a measure of "body size" (the correlation with the log of weight in these samples is 0.93). Size and latitude taken together explain 41.6% of the variation in testis volume among the 42 samples of nonsaltmarsh Savannah Sparrows.

There is a significant correlation between average femur length and average testis volume ($r = 0.55$, $P < 0.01$) (Fig. 1). Testis volume decreases with latitude ($r = -0.35$, $P < 0.05$). The equation describing the

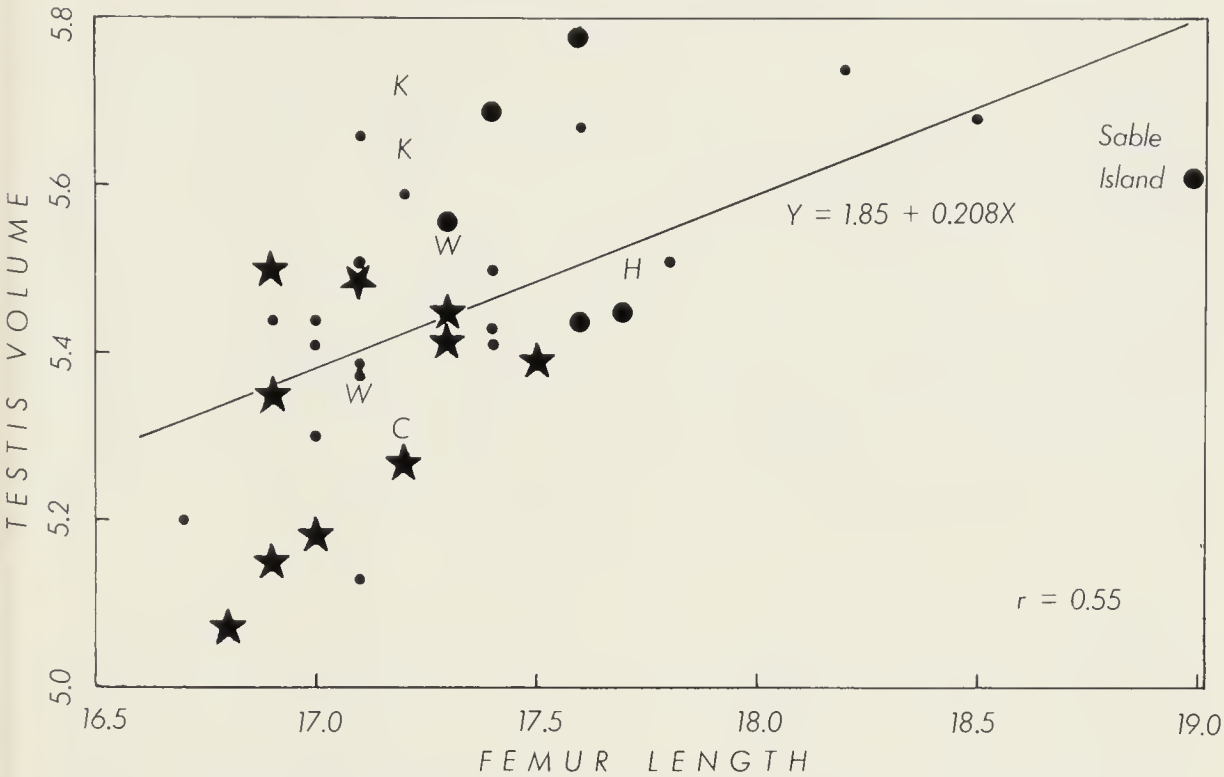

FIG. 1. Relationship between the natural log of testis volume and the average femur length (in mm) among 42 samples of nonsaltmarsh Savannah Sparrows from 40 different localities. Stars indicate the positions of samples of birds that are presumed to be monogamous, and large dots positions of samples presumed to be polygynous. The two "K"s and "W"s indicate the positions of the two samples from Kleinburg, Ontario, and Woodruff, Utah, respectively. "H" and "C" indicate the positions of the samples from Halifax and Churchill; Halifax is a "polygynous" sample and Churchill a "monogamous" one.

relationship of log testis volume as a function of both femur length (FL) and latitude (L) is, $Y = 2.52 + 0.019FL - 0.007L$. Throughout the season monogamous nonsaltmarsh birds consistently have smaller testes than predicted by the combination of body size and latitude, whereas the testis size of the polygynous birds is smaller than predicted early in the year, but appears to increase through the season. Sable Island and Halifax, where polygyny has actually been found to occur regularly, contain birds with testes that average less than predicted by body size and latitude, contra hypothesis. The repeated samples from Kleinburg (K) and Woodruff (W) give an estimation of variation among samples from the same site. Thus, the results of multiple regression using sample means confirm, where comparable, those of the univariate analyses of individuals.

It is not clear why average testis size would decrease with latitude. At high latitudes (e.g., Churchill), Savannah Sparrows are single-brooded, whereas at lower latitudes two or more broods are commonly raised. Among monogamous sparrows it would seem that the sperm demand

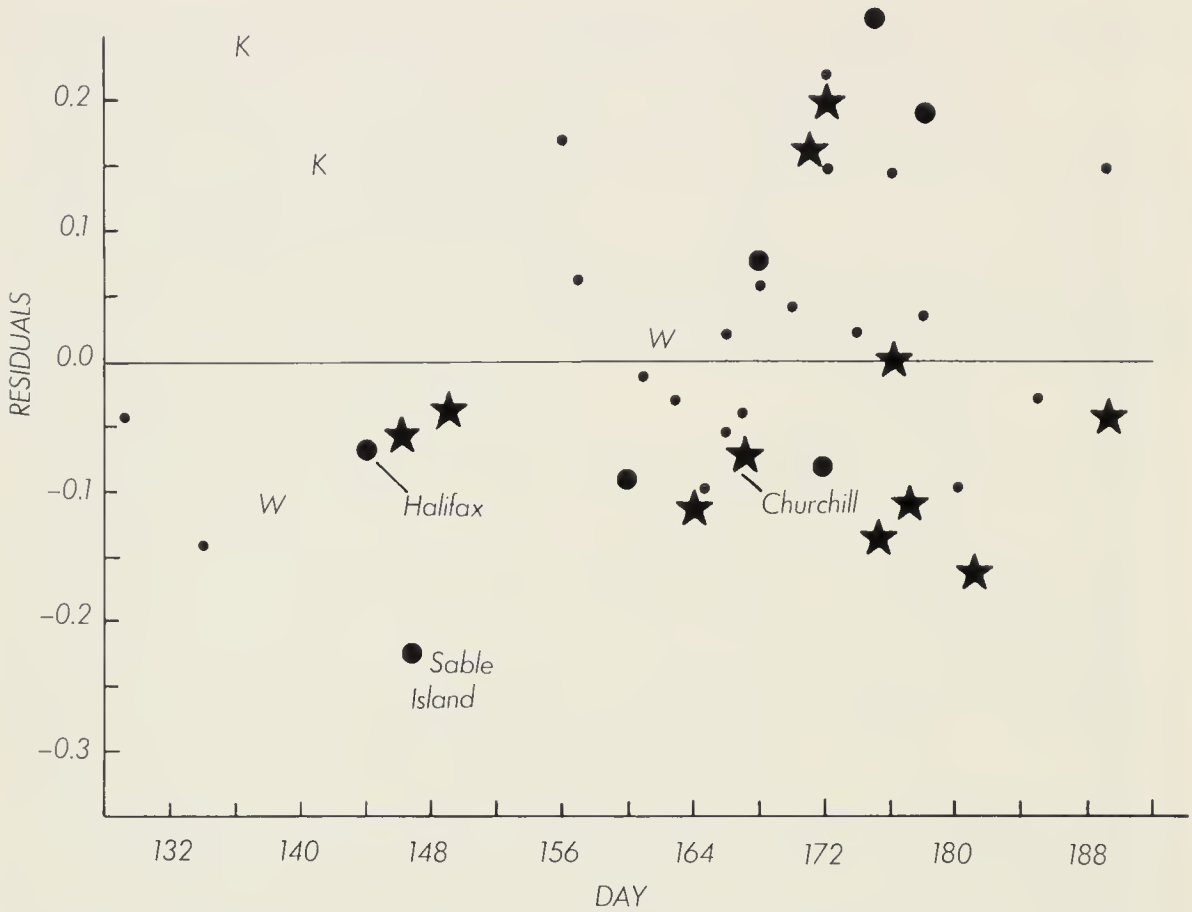

FIG. 2. Relationship between the residuals of samples from multiple regression of testis volume against latitude and femur length, plotted against the day of collection. Overall, the correlation between the residuals and day of collection is not significant. The stars indicate the positions of the 11 samples presumed to be monogamous, and the large dots the positions of the 7 samples presumed to be polygynous. The "W"s and the "K"s indicate the positions of the two samples from Woodruff, Utah, and Kleinburg, Ontario. Day 132 is 12 May, and 188 is 7 July.

during laying would be similar in single- and multi-brooded populations (although the testes would doubtless remain enlarged for a longer period of time in the latter), but perhaps this is not the case.

The relationship between relative testis size and mating system is not clear. As predicted, the testis volume of polygynous males averages greater than that of monogamous males even with the covariation between testis volume and body size accounted for, but the average testis volumes of males from Sable Island and Halifax, Nova Scotia, the only two localities from which polygyny has been found to occur frequently, are smaller than predicted by size alone (Fig. 1) or by the combination of body size and latitude (Fig. 2). Also, 8 of the presumed 11 monogamous samples are from high latitudes, whereas all of the presumed polygynous males are from lower latitude sites. Therefore, the slight differences in the testis

sizes of the polygynous and monogamous males may be an extension of the latitudinal trend.

Saltmarsh Savannah Sparrows have larger testes than their migratory conspecifics (Table 1), and, although there is a great deal of interpopulational variation in size and other features of these birds, relatively large testes are apparently a general characteristic of them (the exceptions, Puerto Peñasco and Magdalena Bay, are based on small samples). Because of their southerly occurrence it seems likely that in all cases they are multibrooded; their mating systems are not known, although they are apparently usually monogamous at Pt. Mugu, California (J. B. Williams, pers. comm.). More knowledge of the breeding biology of these saltmarsh birds is needed.

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SHORT COMMUNICATIONS

Wilson Bull., 99(1), 1987, pp. 73–77

Nesting, voice, status, and relationships of the endemic Cuban Gundlach's Hawk (*Accipiter gundlachi*).—Gundlach's Hawk (*Accipiter gundlachi*) or "Gavilan cabeza grande" is a little known, rare raptor endemic to Cuban woods. Interest in this hawk is considerable because of its threatened status (Brown and Amadon 1970; see also Bond 1968), and its apparent close relationship with the North American Cooper's Hawk (*A. cooperii*) and the neotropical Bicolored Hawk (*A. bicolor*; Brown and Amadon 1970, Wattel 1973). Along with local forestry workers Emilio Diáz R. and Reynaldo Balón D., Reynard, Short, and Alayón studied a nest of Gundlach's Hawk 3 km south of La Munición, elevation about 780 m, 33 km NNE of Guantánamo on 2 and 3 March 1985. To these observations Garrido and Reynard contributed information from past observations and communications with Cuban biologists.

Spectrograms of tape-recordings of the voice of this hawk were made by James Gulledge of Cornell University's Library of Natural Sounds, who also provided comparative data and sonagrams of the Cooper's and Bicolored hawks, as did W. John Smith of the University of Pennsylvania for the Northern Goshawk (*A. gentilis*).

Field observations.—At dusk on 1 March, Reynard heard and tape-recorded (Fig. 1h,i) the squealing call of this hawk, which ceased calling when a Stygian Owl (*Asio stygius*) began to call. On 2 March Reynard detected the Gundlach's Hawk by its loud, harsh series of *Kek, Kek, Kek* . . . calls. Similar vocalizations of a pair of the hawks continued for 5 min. The larger, browner bird, presumed to be the female, was the first to call, the smaller male appearing after about the first minute of her calling. On 3 March Diáz was able to climb the tree and reach the nest, which contained 4 apparently fresh, immaculate (no stains or markings) grayish white eggs. In Garrido's experience the 3–4 egg clutch of this species is the greatest of any Cuban hawk, matched only by the American Kestrel (*Falco sparverius*) among falconiforms.

The nest was 19–20 m up a 25-m tall pine (*Pinus cubensis*) in a "crotch" made by 3 major branches protruding at a 65 to 75° angle from the trunk, spaced around the eastern and southeastern sides of the trunk at the same level. At its base the pine was about 35 cm in diameter, and it was about 15 cm in diameter at the level of the nest. The nest tree was in a dense stand of pines within 40 m of a dirt road frequently used by local woodsmen and their families. The nest measured 70–80 cm in diameter and was 50 cm high, with about a 10-cm deep depression in its center. Construction was entirely of small pine branches and twigs, with a lining of pine bark on which the eggs reposed. One brownish rusty and white barred ventral feather of the hawk was found in the nest. The nest seemed freshly built. The nest and eggs, given intraspecific variation in nest structure and color and markings of eggs, are typical for the Cooper's-Bicolored hawk group.

Both adults were wary, flying in circles at a distance from the observers. They flew with paused wing beats, and approached the nest in an upward glide from below, closing their wings as they landed, as Stone (1899:67) has described for Cooper's Hawks. The male, as well as the female, landed at the nest on several occasions, but at different times. Poor (due to light) but discernible, photographs of the male at the nest, and of the eggs, are on deposit in the American Museum of Natural History.

The surrounding pines comprised a woods about 20 years of age, according to the foresters. The pinewood habitat extends along a small valley (below the nest site) for 3 km to the southeast and 1 km north of the nest. Pines of that size and age are restricted to the east

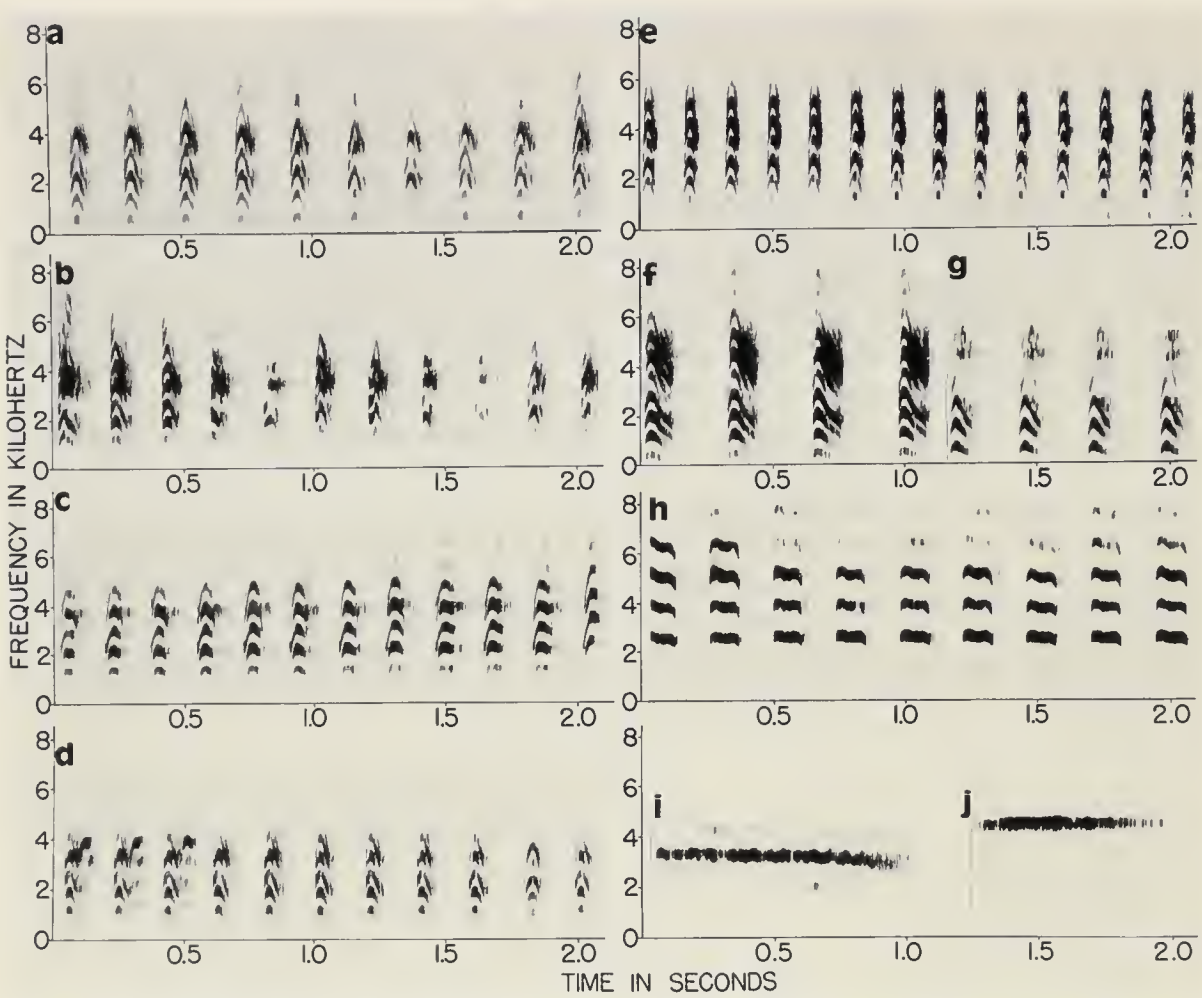

FIG. 1. Spectrograms in wide band pass filter of: (a) *kek* calls, female Gundlach's Hawk; (b) lower pitched *kek* calls of same female as (a); (c) *kek* calls, male Gundlach's Hawk; (d) *kek* calls of female (throughout) and male (first part, 3 notes, each following a female's note) Gundlach's Hawk; (e) *kek* calls of Cooper's Hawk from Arizona, sex unknown; (f) *kek* calls of presumed female Bicolored Hawk of pair, Rio Grande do Sul, Brazil; (g) *kek* calls of presumed male Bicolored Hawk, mate of bird in (f); (h) *kek* calls of Northern Goshawk from Arizona, sex unknown; (i) "squeal" call of Gundlach's Hawk, Zapata Swamp (see text); and (j) "squeal" call of one of nesting pair of Gundlach's Hawks reported in this paper.

side of the steep valley, but a few border the stream 150 m below. Plantings of younger pines occur to the north and east of the site. Dense low, secondary hardwood stands form a tangle in the valley, with a few taller trees reaching 50 m (hardwoods) or 30 m (pines) in height. The nearest habitation is over the limestone scarp bordering the valley, some 700 m west of the nest. Thus the hawks had available to them an extensive area of woods, with some diversity of habitat in the valley and on the surrounding slopes.

Potential competitors seen nearby were a Red-tailed Hawk (*Buteo jamaicensis*) and a Broad-winged Hawk (*B. platypterus*). Some wing feathers of a nighthawk (*Chordeiles* sp.) near the base of the nest tree possibly represent a prey item of the Gundlach's Hawk.

The female was larger and browner than the male Gundlach's Hawk, and both were pale below with markings visible only on the belly. Conspicious were the flaring grayish white flank and undertail feathers against the darker, barred belly and thighs, the equally pale-

and-dark-barred tail, the distinct blackish gray cap of the male, and the pale bill that contrasts with the darker crown.

Status and distribution.—Observations by Garrido and by Carlos Wotzkow, Jorge de la Cruz, and Rogelio García Arencibia (Garrido and Alayón, pers. comm.) in the past decade indicate the presence of small populations of hawks in the Sierra del Rosario of Pinar del Río to westernmost Havana Province, in the Zapata Swamp region of southern Matanza Province (Garrido 1980), and in central-southern Cuba between Laguna Guanaroca in Cienfuegos Province east to the Sierra del Escambray, Sancti Spiritus Province. All of the recent sightings reported by Garrido (1985) are from these three areas (*cf.* Bond 1963:10, 1964:5). There may be isolated pairs or small populations scattered elsewhere in western and central Cuba, as in coastal northern Matanzas Province where Reynard found the hawk (see below) in 1984. Garrido (1976) also has found Gundlach's Hawks on Cayo Coco and Cayo Guajaba off Ciego de Avila and Camaguey provinces, north-central Cuba.

The main center of distribution of Gundlach's Hawks must, however, lie in eastern Cuba between Gibara, Holguín Province on the north coast, the Sierra Maestra on the south coast (Granma, Santiago de Cuba provinces), and eastern Guantánamo Province, where a population was recently discovered near Baracoa. Short saw a displaying, squealing male Gundlach's Hawk near Ojito de Agua, north-central Guantánamo in April, 1986, as well as one of the rarer Sharp-shinned Hawks (*A. striatus*). There are many valleys, hills, and mountains in this region, which are not heavily populated and are rarely visited by ornithologists (Garrido 1985:995). We guess that most of the remaining pairs are to be found in this region, which affords the best chance for long-term survival.

We estimate that no more than about 150–200 pairs remain over the whole island. Disturbance, removal of forest, and persecution by farmers represent the main threats to the species. Overall, it is not as rare (Garrido 1985, pers. obs.) as are the Cuban race of the Sharp-shinned Hawk (*A. s. fringilloides*) and the Cuban Hook-billed Kite (*Chondrohierax* [*uncinatus*] *wilsonii*). Fortunately for it, most tree-planting in Cuba is of indigenous trees, especially pines, rather than exotic trees.

Diet.—There is a suggestion (above) that one of the birds may have eaten a nighthawk. It preys mainly or entirely on birds, including chickens, pigeons, and quail (Gundlach 1871, 1876). Wotzkow (in litt. to Garrido) noted it chasing "parrots." Possibly the large feet of the hawk relate to its feeding on birds of the size of the Cuban Parakeet (*Aratinga euops*), the Cuban Parrot (*Amazona leucocephala*), and the extinct Cuban Macaw (*Ara tricolor*), all birds of its habitat.

Vocalizations.—Two types of calls, the *kek* or "cackle" and the "squeal" were heard and recorded on tape in the nesting area. These represent the 2 main calls of species of *Accipiter,* e.g., the Eurasian Sparrowhawk (*A. nisus*) and Northern Goshawk, as described and figured by Cramp (1980). The Gundlach's Hawk *kek* calls likely were in the form of threat against intruders, among the categories of *kek* calls in Cramp (1980) and Schnell (1958). Both sexes called when perched and in flight, but, typical of the genus, most calls were uttered by the female. There were at least 26 "cackle" bursts, most by one bird, but both individuals called simultaneously 3 times. Noteworthy variation (Fig. 1) involves the number of *keks* per series, tempo, pitch, and loudness, with the female calling at a lower pitch. It will be seen from Figure 1 that the sexes differ markedly in quality, the *kek* of the male being softer, clearer, and with a shallower, longer peak (Fig. 1a–d).

For comparison we include *kek* calls of *A. cooperii* (Fig. 1e, perhaps a male) that resemble *kek* calls of Gundlach's Hawk, but have a faster tempo and notes shorter in duration, and of *A. bicolor* (Fig. 1f,g). The *kek* calls of *A. bicolor* represent a pair recorded by William Belton in Rio Grande do Sul, Brazil. Overall the notes of the Bicolored Hawk are longer with slower delivery than in Cooper's or Gundlach's hawks, but their structure more closely

resembles those of the Gundlach's Hawk. As a group, *A. bicolor, A. gundlachi,* and *A. cooperii* agree more with one another in the low pitch of the fundamental tone and number of overtones in the *kek* call than with their nearest relative, the Eurasian Sparrowhawk (Cramp 1980:166).

The wailing "squeal" call, associated with interactions between the pair (see Cramp 1980 for Northern Goshawk and Eurasian Sparrowhawk) was recorded on tape 1 March (Fig. 1j). Reynard previously had recorded the same type of call (Fig. 1i) on 13 March 1984 in a wooded area at Cienaga de Zapata. Northern Goshawk and Eurasian Sparrowhawk wails are lower pitched than Gundlach's Hawk "squeals" (Cramp 1980:166, Bergmann and Helb 1982:83).

Taxonomy and zoogeography.—We are satisfied that the Gundlach's Hawk represents a valid species related to both the Cooper's and Bicolored hawks, forming a superspecies with them, as concluded by Brown and Amadon (1970) and Wattel (1973). Gundlach's Hawk resembles the Bicolored Hawk (particularly *A. bicolor chilensis* and *A. b. guttifer*) rather than the Cooper's Hawk in its grayish breast color without markings, more heavily rufous-barred belly and thighs, and lack of a conspicuous pale area on the side of the neck to the nape. Its "cackle" call tends toward the noisier, less clear "cackle" of the Cooper's Hawk and those of the Northern Goshawk and Eurasian Sparrowhawk.

Gundlach's Hawk resembles the Cooper's Hawk and differs from the Bicolored Hawk in its tail barring. Cooper's Hawks are more sexually dichromatic than the Bicolored Hawks, and Gundlach's Hawks are even more dichromatic. However, the very strong legs and feet of Gundlach's Hawk, its pale bill, the underwing spotting of immatures, and its large size are distinctive. If it were an extreme southeastern race of Cooper's Hawk, one would expect it to be smaller than more northern populations, but it is larger than Cooper's Hawks (and Bicolored Hawks). Cuban Broad-winged Hawks, Sharp-shinned Hawks, American Kestrels, and most Cuban birds representing North American species are smaller than their mainland relatives. Taken together, along with differences in color of the breast and thighs, lack of the neck marking and vocal divergence (all in the direction of the Bicolored Hawk), these traits argue for the recognition of Gundlach's Hawk as a full species related closely to both Cooper's and Bicolored hawks.

We conclude that this accipitrine has been on Cuba for a long time, evolving its unique features and combination of features in response to the environment there, particularly, available prey and raptorial competitors. The dearth of raptorial birds of similar size and habits may be related to its large size and the gap in size between it and the very small *A. striatus fringilloides* on Cuba. The 3 continental North American accipiters show a sharp difference in size, including intraspecific size differences between sexes within each species. Neotropical *A. bicolor* exists with a number of potentially competitive large hawks (and falcons), as well as smaller congeners (e.g., *A. poliogaster, A. striatus*). Such competitive pressure seems considerably less for Gundlach's Hawk (only the very different *Buteo platypterus* is similar to it in size) than for its mainland relatives.

We can offer no clue as to whether ancestral *A. gundlachi* reached Cuba from North America or Middle America, and consider either derivation as likely as the other. Wattel (1973:128) argued that it is futile to pursue "the question whether *A. gundlachi* is more closely related to *A. cooperii* or to *A. bicolor.*" In view of the diverse features characterizing Gundlach's Hawk, and the possibility that it could have reached Cuba from Middle America as well as from North America, we concur.

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Postfledging behavior of American Kestrels in southwestern Quebec.—Postfledging dependency in the American Kestrel (*Falco sparverius*) lasts a minimum of 2–4 weeks, during which time the young gradually develop hunting skills and agility in flight (Balgooyen 1976). Anecdotal reports by Sherman (1913), Wheeler (1979), and Sherrod (1983) suggest that

TABLE 1

NUMBER OF 10-MIN SEGMENTS DURING WHICH FLEDGLING AMERICAN KESTRELS ENGAGED IN SOCIAL AND NONSOCIAL BEHAVIOR

	Days postfledging			
	1–5	6–10	11–15	16–20
Social behavior	10 (14.7)[ab]	25 (19.6)[b]	8 (15.3)[b]	14 (7.5)[b]
Nonsocial behavior	41 (36.3)	43 (48.4)	45 (37.7)[c]	12 (18.5)[b]

[a] Observed (expected, if no change occurred over time).
[b] $P < 0.001$, analysis of standard residuals.
[c] $P < 0.01$, analysis of standard residuals.

some family groups may remain intact for months after leaving their territory, possibly even migrating together. Balgooyen (1976) reported that young kestrels disperse singly, possibly in order of age. Cade (1955) observed hunting bands of 10–20 juveniles and speculated that siblings leave the natal territory as a group and merge with other groups of siblings. Wheeler (1979) sighted postbreeding hunting groups of up to 14 adults and juveniles. Wilmers (1982) observed postbreeding groups of unknown age composition frequenting areas that had not been included in breeding territories that season. Here we examine the behavior of adult and recently fledged young kestrels, in particular the social behavior of the young.

Study area and methods.—The study area, 20 km west of Montreal, Quebec, is characterized by agricultural fields interspersed with small stands of northern hardwoods. Kestrels nest in natural cavities and artificial nest boxes throughout the area.

The 3 kestrel families we studied during the 1984 breeding season nested in boxes. Four young apiece fledged from Nests I and III. Three young fledged from Nest II; the adult male was removed from the latter nest 5 days before the first egg hatched as part of another study (Bowman 1985).

We color-marked all young at approximately 22 days after hatching by treating the tips of their primaries or rectrices with a paste of 30% hydrogen peroxide and Germaine Monteil Creme D'lite® bleach for human hair. The marking method was tested on captive-bred fledgling kestrels prior to use in the field. Bleaching was not associated with feather breakage, loss of barbule function, behavioral aberrations, or mortality in either captive or wild birds.

Lett observed each nest for 1 h daily from 100 m with 8× binoculars and a 45× telescope. Observations began one week before the expected fledging date and ended when no young had been observed within sight of the nest for 5 consecutive days. One third of the observations at each nest took place in the morning, ⅓ in the afternoon, and ⅓ in the evening. Due to between-nest differences in the timing of fledging and dispersal, we performed statistical tests on 15 h (=5 days) of prefledging and 60 h (= 20 days) of postfledging observations out of a total 102 h. We subdivided each hour of observation into 6 10-min segments. We grouped the observations into 5-day blocks arranged so that day 1 is the first day on which any of the nestlings left a given nest box.

Results.—The behavior of fledgling and adult kestrels differed in several respects. Fledglings perched in thick, concealing foliage for 68% (N = 90) of the time segments during the first 5 days postfledging. During the same 5-day period, adults spent 76% (N = 90) of the time segments flying near the nest or perched on high, exposed snag tops, dead branches, and utility wires. In the first 5 days postfledging, 92% (N = 25) of flights made by young birds were direct flights from one perch to another (<35 m apart). Fledglings occasionally caught their wings in branches when landing or missed the perch altogether. Fledglings

attempted to hover (cf. Balgooyen 1976) only on windy days, but were unable to maintain their position. In general, fledgling flight lacked the smooth, controlled appearance of adult flight. Fledglings gave the food-begging call, which resembles the adult "whine" vocalization (Willoughby and Cade 1964), for up to 10 min at a time, either when perched or when flying towards a parent. No adult "whine" calls were heard during the postfledging period.

We defined any behavior that brought two or more fledglings within 2 m of one another as social. Aggressive social behaviors included pecking, footing, vigorous billing, flying at and flushing, and snatching (or attempting to snatch) food from siblings. Nonaggressive social behavior included perching close together, simultaneous preening, and flying to join one or more perched siblings. Sibling chases were considered social behavior, but were not classified with regard to aggression. Nonsocial behavior was defined as any activity performed at a distance >2 m from the siblings (e.g., hunting). The proportion of time spent on social and nonsocial behavior varied over the postfledging period ($\chi^2 = 17.02$, df = 3, $P < 0.001$) (Table 1). Nonsocial behavior occupied the bulk (71%, N = 198) of the time segments in which fledglings were present and active. Social behavior was usually nonaggressive (81%, N = 57), although aggression (16%, N = 57) and sibling chases (7%, N = 57) also occurred. Aggression was more likely to occur during time segments when food was present (binomial test, $P < 0.05$) and during segments with nonaggressive behavior between siblings (binomial test, $P < 0.01$). Aggressive interactions typically followed prey delivery to one of two fledglings that were perched close to each other.

Parental prey deliveries differed significantly over time ($\chi^2 = 19.37$, df = 4, $P < 0.001$) (Fig. 1a), and peaked at days 6–10. The same was true for the time spent by the young in calling for food ($\chi^2 = 12.48$, df = 3, $P < 0.01$) (Fig. 1a). Adults responded to 15% (N = 198) of the fledglings' food begging calls by giving the excited, potentially aggressive "klee" vocalization (Willoughby and Cade 1964). The only clear instance of adult aggression toward offspring occurred when an adult female rose vertically off a perch to bump a begging fledgling. Young kestrels occasionally flew toward their parents and briefly hovered above them or flushed them from perches and chased them. This aggressive begging behavior (cf. Sherrod 1983:126) was largely limited to Nest II (91%, N = 11 incidents). Most of the aggressive begging (55%, N = 11) (Fig. 1a) occurred at 11–15 days, just as the frequency of parental prey deliveries began to decline. Fledgling-parent aggression, however, was no more frequent in time segments when food was absent than when present (binomial test, $P = 0.25$). Parents began to leave the nest area on the approach of their young at days 6–10, and most instances of parental avoidance of the young (83%, N = 12) (Fig. 1a) took place between days 11 and 20.

Seventy-one percent (N = 14) of the attacks by adult kestrels on other birds were directed at Northern Harriers (*Circus cyaneus*), which are reported to prey on kestrels (Bent 1937). Attacks peaked at days 1–5 (Fig. 1b). The amount of time adults were observed within sight of the nest varied significantly ($\chi^2 = 39.98$, df = 4, $P < 0.001$) (Fig. 1b) over the late nestling and postfledging periods, with a parent in attendance during 71% (N = 270) of the time segments between 5 days prefledging and 10 days postfledging and during 31% (N = 180) of the segments between days 11 and 20.

An unmarked juvenile female first appeared at Nest II on day 10. She elicited no observable response from the resident birds, although she flew within 50 m of the adult female. At Nest I on day 14, an unrelated juvenile female and the resident adult male briefly flew around each other with the fluttering wingbeat characteristic of courtship flights (cf. Balgooyen 1976) as the male gave the "chitter" call commonly used in interactions between mates (Willoughby and Cade 1964). At Nest II on day 24, an unrelated juvenile male flew, perched, and preened with two of the female fledglings. He also approached the adult female and displaced her from her perch. On day 28, a young male from Nest I was seen flying side by side with an

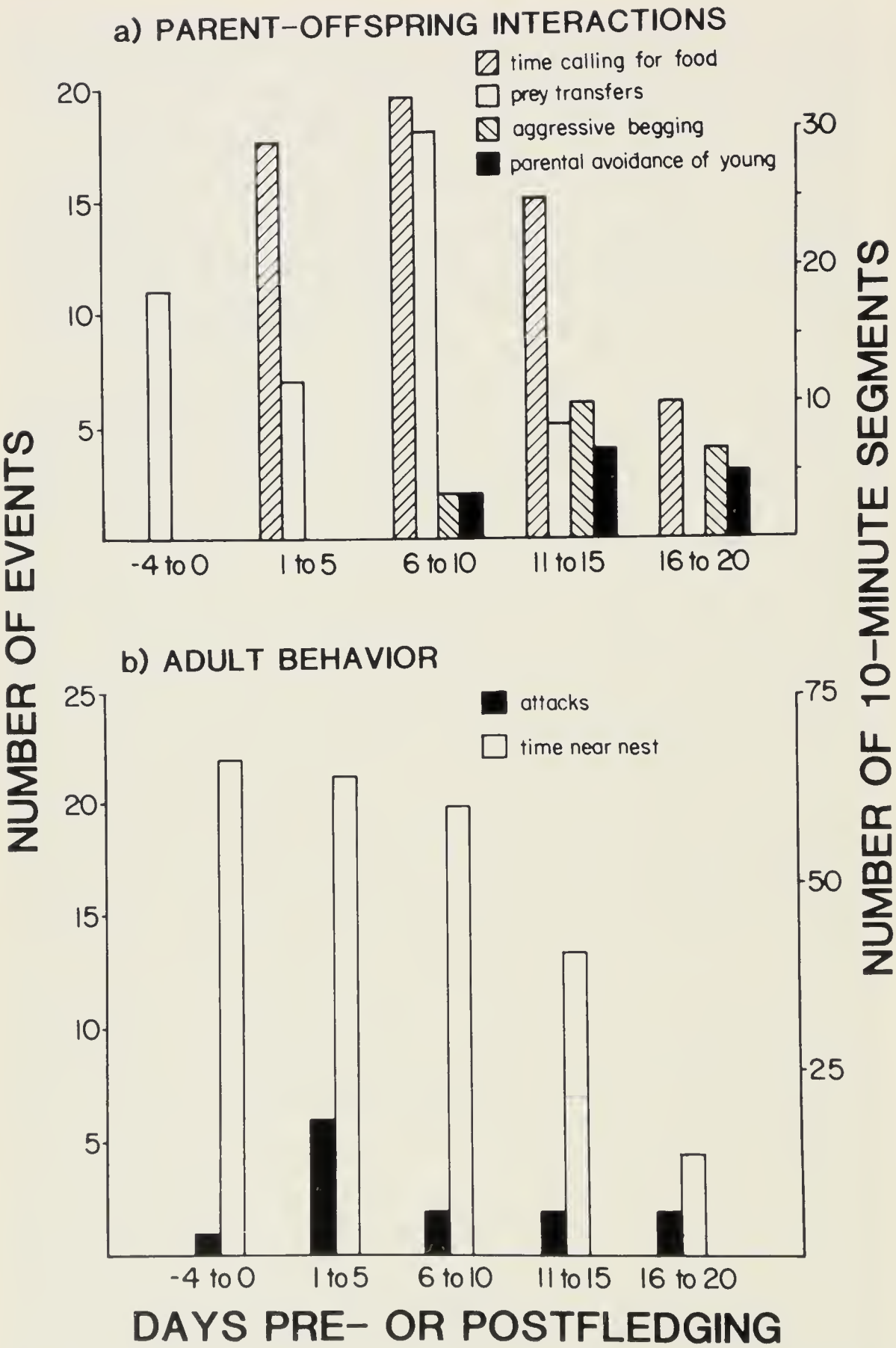

FIG. 1. a. Parent-offspring interactions and days pre- or postfledging. b. Anti-predator behavior of adults and days pre- or postfledging. Behavioral patterns are defined in the text.

unmarked juvenile female over a territory from which neither had fledged. In all cases where adults were present, they refrained from the behavior Cade (1955) associated with territorial defense against conspecific individuals, i.e., klee-ing, stooping, striking, and chasing. When fledglings interacted with unrelated juveniles, their behavior was indistinguishable from the nonaggressive interactions among siblings.

Discussion.—Although Newton (1979) contended that most fledgling raptors perch apart from their sibs, young American Kestrels follow and perch near their sibs and engage in social behavior. Fledglings of several other raptorial birds also follow siblings from perch to perch (Southern et al. 1954, Johnson 1973, Parker 1975, Sherrod 1983). Nestlings and fledglings of birds of prey have been observed joining in activities initiated by siblings (Herrick 1924, Bond 1942, Johnson 1973, Parker 1975, Kussman 1977, Sherrod 1983), similar to the socially facilitated preening bouts we observed in kestrels.

Many young raptors behave aggressively toward both siblings and parents in the presence of food (Rowe 1947, Schnell 1958, Meinertzhagen 1964, Johnson 1973, Kussman 1977, Jenkins 1978, Sherrod 1983). Fledgling kestrels, however, are rarely aggressive toward either siblings or parents, and the only aggression that we saw among siblings was associated with the presence of food.

Our observations of interactions between known individuals and unrelated juveniles support Balgooyen's (1976) finding that adult kestrels tolerate intrusions by dispersing juveniles into their territories. The presence of only one unrelated juvenile at a time suggests that young kestrels need not disperse in the company of their siblings (cf. Cade 1955). We suspect that families with fledged young may be attractive to dispersing juveniles, and that fledglings may disperse in the company of a juvenile which has intruded on their natal territory. Further observations of dispersing juveniles are necessary to clarify the process by which unrelated kestrels form the large postbreeding aggregations described by other workers.

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Abundance, habitat use, and perch use of Loggerhead Shrikes in north-central Florida.—Although populations of Loggerhead Shrikes (*Lanius ludovicianus*) have declined severely in numbers in many parts of their range in the United States (Morrison 1981, Fraser and Luukkonen 1986), they remain common in Florida. I studied relative abundance, habitat use, and perch use of Loggerhead Shrikes in north-central Florida. These data should provide useful comparative information not only for future studies in this area, but for other regions where shrike populations are low.

I randomly established 24 16-km roadside transects on paved secondary roads in parts of nine counties surrounding Gainesville, Florida (see Bohall 1984 for details). Two observers censused each transect once every 2 weeks from 18 October 1981 to 30 October 1982, by driving 32 km/h and scanning both sides of the road for perched and flying shrikes. I recorded the habitat for each shrike observed, whether the bird was on the roadside or actually in the habitat, and the perch type.

I combined 26 recognized vegetation types on the basis of vegetation structure into 5 habitat types for data analyses: completely open areas (low herbaceous vegetation without trees), midsuccessional (overgrown areas with tall shrubs or small trees), woods, wetlands (marsh or lake edge), and pastures with scattered trees. The completely open areas included settled areas (suburbs, lawns, homes), improved pasture, overgrown pasture (herbaceous

TABLE 1

NUMBER OF LOGGERHEAD SHRIKES OBSERVED IN 5 HABITATS ALONG 24 16-KM ROADSIDE TRANSECTS IN NORTH-CENTRAL FLORIDA

Habitat	Observed	Expected	$\bar{P}_i$[a]	P_i[b]	95% Confidence interval[c]
Open	1456	594	0.877	0.358	$0.856 \leq P \leq 0.897$
Midsuccessional	43	78	0.026	0.047	$0.016 \leq P < 0.036$
Scattered trees	112	99	0.067	0.060	$0.052 \leq P < 0.083$
Woods	44	883	0.026	0.531	$0.016 \leq P \leq 0.037$
Wetlands	6	7	0.004	0.004	$-0.0002 \leq P \leq 0.007$
Total	1661	1661			

[a] Proportion of shrikes observed in each habitat (for example: 0.877 = 1456/1661).
[b] Proportion of total habitat available (used to calculate expected values; for example: 594 = 0.358 × 1661).
[c] 95% Confidence interval around proportion of observed shrikes. If P_i does not fall within this interval, observed use is significantly less than or greater than expected.

vegetation ≤ 1 m in height), and crop fields (planted and unplanted). I measured the linear distance of habitat types on either side of the road with an odometer and calculated the percentage availability of each.

I evaluated habitat use with Chi-square tests for goodness-of-fit and calculated a 95% confidence interval to determine if a given habitat was used significantly more or less than expected (Neu et al. 1974). Expected values were calculated using percentage habitat availability. Winter (18 October 1981 to 20 March 1982 and 19 September to 30 October 1982) and summer (21 March to 18 September 1982) habitat use was compared with a Chi-square contingency test. Perch use was evaluated with Chi-square tests for goodness-of-fit and contingency.

I observed 965 shrikes (68.9 per 2-week sampling period) in winter, and 697 (53.6 per sampling period) in summer. The winter population was significantly larger than the summer population ($\chi_1^2 = 25.7$, $P < 0.001$).

I found no significant difference in use of the 5 habitat types between winter and summer ($\chi_4^2 = 4.63$, $P > 0.30$), so I combined data from the 2 seasons. Habitat use of shrikes observed along the roadside was not significantly different from that of shrikes observed in habitats away from the roadside ($\chi_4^2 = 1.50$, $P > 0.80$), indicating that samples of shrikes along the roadside did not bias the overall results of habitat use. The observed use of the 5 habitat types was significantly different from expected based on availability ($\chi_4^2 = 2065$, $P < 0.001$) (Table 1). Shrikes used open areas significantly more than expected and mid-succesional areas and woods significantly less than expected. Pastures with scattered trees and wetlands were used in proportion to their availability. Similarly, Bent (1950) has stated that shrikes are open country birds.

Use of the 4 open habitat vegetation types also was significantly different than expected ($\chi_3^2 = 99.02$, $P < 0.001$) (Table 2). Settled areas were used significantly less by shrikes than expected, possibly due to more human disturbance there. Improved pastures were used significantly more than expected. The very low vegetation there may facilitate sighting and capture of prey. I observed shrikes more than expected in overgrown pastures and as often as expected in crop fields. However, of the 171 shrikes in crop fields, 74% were observed along the roadside. Similarly, 66% of the 192 shrikes observed in overgrown pastures were associated with the roadside. In improved pastures, 54% (N = 944) of the shrikes observed

TABLE 2

NUMBER OF LOGGERHEAD SHRIKES OBSERVED IN 4 OPEN HABITAT VEGETATION TYPES ALONG 24 16-KM ROADSIDE TRANSECTS IN NORTH-CENTRAL FLORIDA

Open habitat vegetation types	Observed	Expected	$\bar{P}_i$[a]	P_i[b]	95% Confidence interval
Settled	149	299	0.102	0.205	$0.082 \leq P \leq 0.122$
Improved pasture	944	854	0.648	0.587	$0.617 \leq P \leq 0.680$
Overgrown pasture	192	149	0.132	0.103	$0.110 \leq P \leq 0.154$
Crop fields	171	154	0.117	0.106	$0.096 \leq P \leq 0.138$
Total	1456	1456			

[a] Proportion of shrikes observed in each habitat.
[b] Proportion of total habitat available (used to calculate expected values).

were along the roadside. In crop fields, prey may be less available than in improved pastures, and the tall vegetation of overgrown pastures may hinder sighting and capture of prey. In contrast, vegetation along the roadside was very similar to improved pastures. Mills (1979) reported that shrikes preferentially hunted in short vegetation. Siegel (1980) and Kridelbaugh (1983) reported on the importance of pastures within the breeding habitat of shrikes, and Porter et al. (1975) found shrikes using grasslands more than cultivated fields.

Most shrikes I observed were perched on powerline wires (Table 3). In Texas, 98% of the perched shrikes observed by Bildstein and Grubb (1980) were on powerlines. In general,

TABLE 3

NUMBER OF PERCHED AND FLYING LOGGERHEAD SHRIKES AND PERCH-SITE USE ALONG 24 16-KM ROADSIDE TRANSECTS IN NORTH-CENTRAL FLORIDA

Location	N	%
Manmade perches		
Powerline wire	1027	61.8
Utility pole	19	1.1
Fencewire	101	6.1
Fencepost	221	13.3
Subtotal	1368	82.4
Natural perches		
Live tree	41	2.5
Dead top of live tree	28	1.7
Bare tree, snag	76	4.6
Shrub	89	5.4
Fallen tree, debris, ground	28	1.7
Subtotal	262	15.8
Flying	31	1.9
Total	1661	100.0

manmade perches were used significantly more often than natural perches ($\chi_1^2 = 461.57$, $P < 0.001$), probably because fences and powerlines often were the only perches available in large open pastures.

High perches (powerlines, utility poles, live and dead standing trees) were used more often than low perches (fenceposts, fencewire, shrubs, fallen trees) in summer (81% vs 19% of observations, N = 677, $\chi_1^2 = 256.85$, $P < 0.001$) and winter (68% vs 32%, N = 953; $\chi_1^2 = 117.76$, $P < 0.001$). There was, however, a significant increase in use of high perches from winter to summer ($\chi_1^2 = 35.16$, $P < 0.001$). Shrikes may perch higher during the summer to be more conspicuous during the breeding season. Morrison (1980) reported that shrikes selected higher perches during the summer in response to the greater height and density of vegetation. In Florida, vegetation in improved pastures remains low in summer, and shrikes tended to perch low more frequently there. Mills (1979) suggested, based on optimal foraging models, that American Kestrels (*Falco sparverius*) perch high when hunting large prey and perch low when foraging for smaller prey. Perhaps shrikes use a similar strategy. Alternatively, shrikes may perch lower in winter for more efficient thermoregulation.

These data on the relative abundance, habitat use, and perch use of Loggerhead Shrikes in an area where their numbers are relatively high will establish important baseline data for subsequent studies. They may also be of use when compared to data collected by researchers conducting studies in other parts of the Loggerhead Shrike's range where they are less common or declining where habitat use may not represent the habitat potentially used by a healthy population.

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Testosterone, aggression, and dominance in Gambel's White-crowned Sparrows.—The effects of testosterone on dominance hierarchies differ among avian species, and it is difficult to predict how particular species will respond. Selinger (1967) found that androgen injections increased the number of head grabs and pecks in Japanese Quail (*Coturnix coturnix japonica*), in some cases leading to a reversal in dominance. Androgen injections also led to a reestablishment of original dominance relationships in quail that had previously lost their dominance due to castration. Gottier (1968) reported that chickens (*Gallus gallus*) injected with androgens moved up in their hierarchy. In the polymorphic Harris Sparrow (*Zonotrichia querula*) darker birds are dominant to lighter colored birds (Rohwer, 1978). Low-ranking birds disguised to resemble high-ranking individuals by painting did not move up in the hierarchy, unless they were also treated with testosterone (Rohwer and Rohwer 1978). Testosterone injections, however, had no effect on low-ranking Red-billed Queleas (*Quelea quelea*), European Starlings (*Sturnus vulgaris*), or domestic Rock Doves (*Columba livia*) (Mathewson 1961, Crook and Butterfield 1968, Lumia 1972).

Here we report on post-testosterone treatment hierarchies in migratory Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*).

Methods.—In the fall of 1979, hatching-year Gambel's White-crowned Sparrows (aged by crown color) were captured in the Los Angeles, California area, sexed by laparotomy, and held for several weeks in outdoor aviaries. On 9 January 1980, control and experimental groups of six males each were color-banded for individual recognition and put in separate rooms in 1.2 × 0.9 × 0.5 m cages. Photoperiod was held at 10L:14D and room temperature at 20 ± 1°C. Birds were fed seeds, pheasant starter, grit, greens, and vitamins. From 13 January through 28 January (Period 1) each of us independently observed the two captive flocks. For 1 h each observation morning we counted displacements as described by Parsons and Baptista (1980). We then compared our tabulations. Because we found that we agreed on the positions of the birds in the two hierarchies, we pooled our data throughout the experiment. On 28 January the two lowest ranking birds in one hierarchy (birds 5e and 6e in the experimental group) were given intramuscular injections of testosterone (Searle SC-16148, 0.15 cc at 50 mg/cc). Previously, this dosage was found to be effective in inducing song (Baptista 1974) (see below). Birds 5c and 6c in the control group were injected with placebo (the peanut oil vehicle). Four days later birds 5 and 6 in the experimental group were given a second injection (0.10 cc), and their counterparts in the control group were injected with placebo. We observed the birds for 45 days, during which time 4819 aggressive interactions were recorded (2181 in the control group and 2638 in the experimental group).

Observations were made between 13 and 28 January. Before injections, straight-line hierarchies were established in both groups (Period 1) (Fig. 1). The ratio of wins to losses between any two birds indicates which of the two is dominant, although subordinate birds occasionally won encounters with dominants.

Behavior following injections.—In the control group, no changes in behavior occurred after placebo injections of the two lowest ranking birds (5c and 6c). In the experimental group, three types of changes were observed. First, the injected birds, 5e and 6e, initiated

Period 1 Jan. 13 – Jan. 28

Losses — Group 1 (Control)

Wins	1c	2c	3c	4c	5c	6c	Individual Percent Wins
1c		24	20	9	6	7	85.7
2c	7		85	25	26	28	87.2
3c	3	1		100	124	57	73.1
4c					4	5	6.3
5c				1		15	9.0
6c	1				1		1.8

Losses — Group 2 (Experimental)

Wins	1e	2e	3e	4e	5e	6e	Individual Percent Wins
1e		22	8	18	9	3	87.0
2e	1		50	112	51	25	88.2
3e	5	4		77	61	18	73.7
4e	1	3	1		78	71	42.0
5e	2	3		4		64	26.8
6e				2			1.1

Period 2 Jan. 29–Feb. 1 and Period 3 Feb. 2–Feb. 5

Losses — Group 1 (Control)

Wins	1c	2c	3c	4c	5c	6c	
1c		33	6	16	10	3	90.7
2c	2		62	54	37	18	83.6
3c	2			104	95	55	79.0
4c	2	1			9	4	8.4
* 5c	1					6	4.4
* 6c							0.0

Losses — Group 2 (Experimental)

Wins	1e	2e	3e	4e	5e	6e	
1e		8	3	6	10	0	67.5
2e	3		5	56	6	13	37.4
3e		40		76	67	39	93.7
4e	2	16			34	30	36.9
* 5e		52	5	2		103	58.1
* 6e	8	23	2				15.1

Period 4 Feb. 6–Feb. 21

Losses — Group 1 (Control)

Wins	1c	2c	3c	4c	5c	6c	
1c		35	30	40	3	30	63.0
2c	2		66	66	49	31	84.6
3c	5	4		162	142	115	81.7
4c	6				10	6	7.6
* 5c	68					20	30.0
* 6c					1		0.5

Losses — Group 2 (Experimental)

Wins	1e	2e	3e	4e	5e	6e	
1e		8	7	12	18	0	46.4
2e	27		48	97	1	7	37.3
3e	2	1		94	64	58	79.1
4e					90	89	46.6
* 5e	2	214	3	2		90	64.3
* 6e	21	79					29.1

(* indicates injection)

FIG. 1. Dominance hierarchies of control (left column) vs experimental (right column) groups of White-crowned Sparrows. Period 1 illustrates hierarchies before injections. Individual percent wins appear in the column to the right of each hierarchy. Periods 2 and 3 (combined) illustrate hierarchies after injection with testosterone or placebo. Asterisks denote injected birds. Period 4 illustrates the hierarchy beginning 4 days after the second injections.

many more aggressive encounters than they had prior to treatment. Second, they won a much higher percentage of interactions in the total time span following injections than they had before injections (Fig. 2), and several reversals in dominance relationships occurred (Fig. 1). The third change involved the nature of interactions between the two injected birds and their cage-mates. Following androgen treatment, 5e and 6e often pulled at the wings

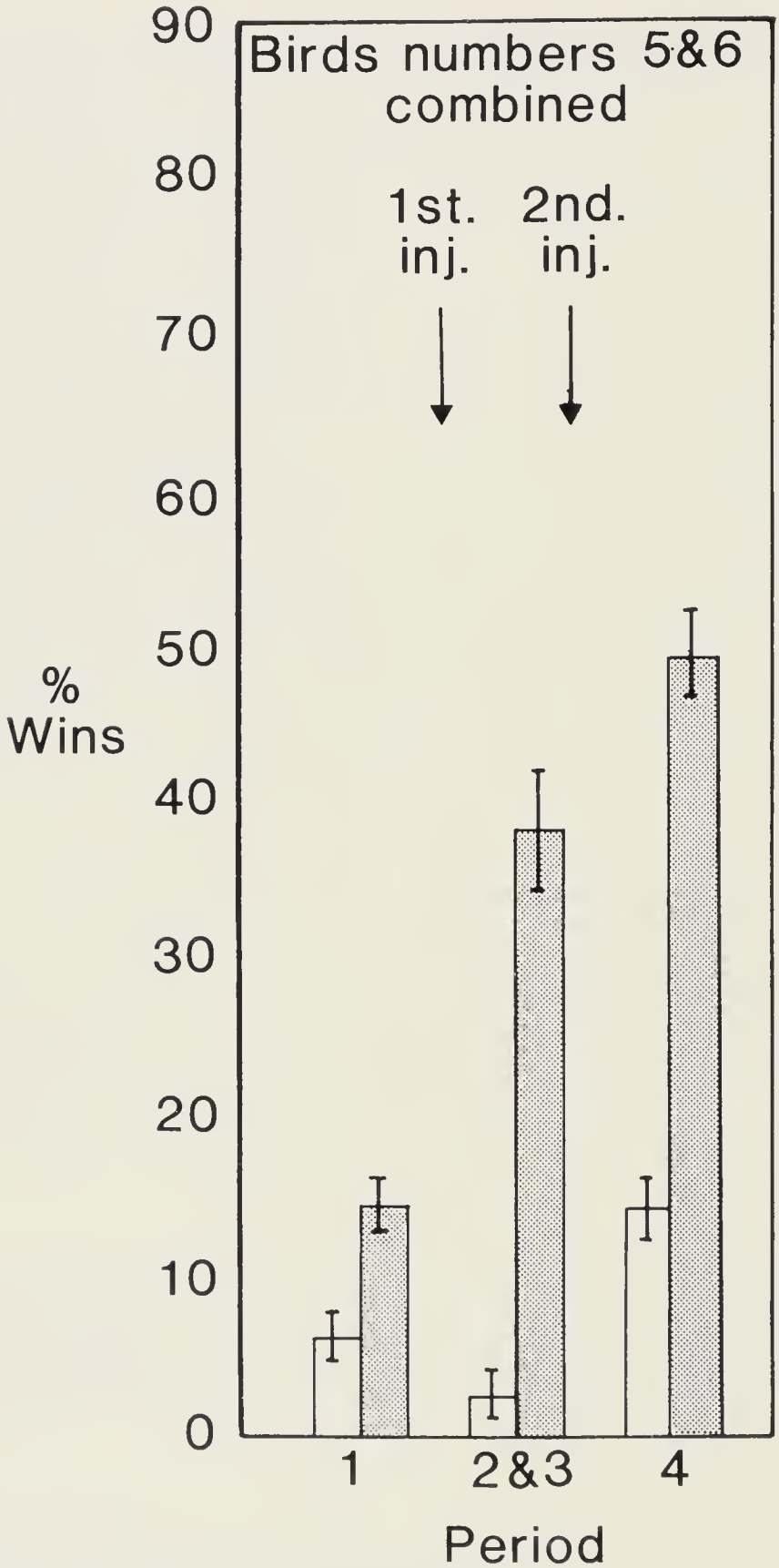

FIG. 2. Percentage of wins of injected birds 5e and 6e combined (gray bars) versus control birds 5c and 6c combined (open bars). Each bar represents the mean ± SE percentage of wins over total number of encounters in which these birds were involved.

and tails of their opponents. This high-intensity aggressive behavior was rarely exhibited by any bird before injections. No wing or tail pulling was observed in the control birds (5c and 6c) during Periods 1 to 3. During Period 4 the mean number of wing or tail pulls in the control groups was 0.2 per day. No wing or tail pulling was observed in the experimental group (5e and 6e) during period one. Following androgen injection, however (Periods 2 and 3), the mean number of wing or tail pulls in the experimental group increased to 4.5 per day. During Period 4 wing and tail pulling in the experimental group was maintained at a rate of 1.4 per day, a higher level than that observed in the control group (0.2 per day). These data contrast with those for pigeons. No increased aggression was found by Lumia (1972) in testosterone-treated low-ranking pigeons, which are strongly influenced by prior experience.

Our observations suggest that, following testosterone treatment, subordinates may direct attacks at cage-mates regardless of rank. This may result in temporary persecution by the dominant. Reversals in rank may ensue. For example, from 6 to 21 February, Bird 6e, originally the bottom-ranking bird, won 79 of 86 encounters with the previously 2nd-ranked bird, 2e (Fig. 1).

In Period 4 the androgen-injected birds remained intensely aggressive. Bird 5e won 214 out of 215 encounters with 2e, and 6e remained dominant to 1e and 2e (Period 4) (Fig. 1). Also, the number of encounters in the control group that fell outside a straight-line hierarchy increased over those in Periods 1 to 3. For example, 5c won 68 out of 71 encounters with 1c (Fig. 1). We have no explanation for these changes, although changes in dominance hierarchies may be spontaneous (Marler 1955), and they have been observed in late winter-early spring in several species (Samson 1977, Parsons and Baptista 1980).

How may the effects of changing season be separated from those of actual androgen injections? We computed the number of interactions won by the fifth and sixth-ranking birds (combined) in control and experimental groups as a percentage of the total number of encounters in which these birds were involved. In Periods 2 and 3, following injections, experimental birds 5e and 6e won more than twice the percentage of encounters that they won in Period 1, before injection (38.6 vs 14.5%). In contrast, in control birds (5c and 6c) the percentage of wins in Periods 2 and 3 was lower than in Period 1.

Hierarchy after metabolism of injected testosterone.—We know from observations that birds treated with androgens initiate many more encounters and that they may rise in dominance status. But what happens *after* the artificially introduced androgens have been metabolized?

Ramenofsky (1984) studied dominance relationships of male Japanese Quail by subjecting them to short-term dyadic encounters in a round-robin tournament over 19 days. Radioimmunoassays indicated that high plasma testosterone levels were correlated with fighting success only in the earlier encounters. By day 15 testosterone levels of winners and losers were similar. She concluded that higher androgen levels influenced the outcome of initial encounters, but that learned response biases took precedence once dominance relationships stabilized. Our study indicates that testosterone injections may effect reversals of dominance in a White-crowned Sparrow flock, but that testosterone is not required to maintain the new hierarchical relationships as developed below.

We noted in earlier studies (unpubl. data) that White-crowned Sparrows engaged in long bouts of whisper singing after testosterone treatment. In this study we counted songs of birds 5 and 6 in both groups in the early afternoon of each observation day. We use rate of whisper singing (cf. Baptista 1974) as a crude index of changes in testosterone levels. Singing by a control bird was heard on only one occasion, before placebo injection. In contrast, on the days following injections with androgen, experimentals 5e and 6e sang frequently. For example, bird 5e sang over 60 songs per half-h following injections (Fig. 3). By Period 4 the amount of singing decreased, probably corresponding with the decrease of synthetic andro-

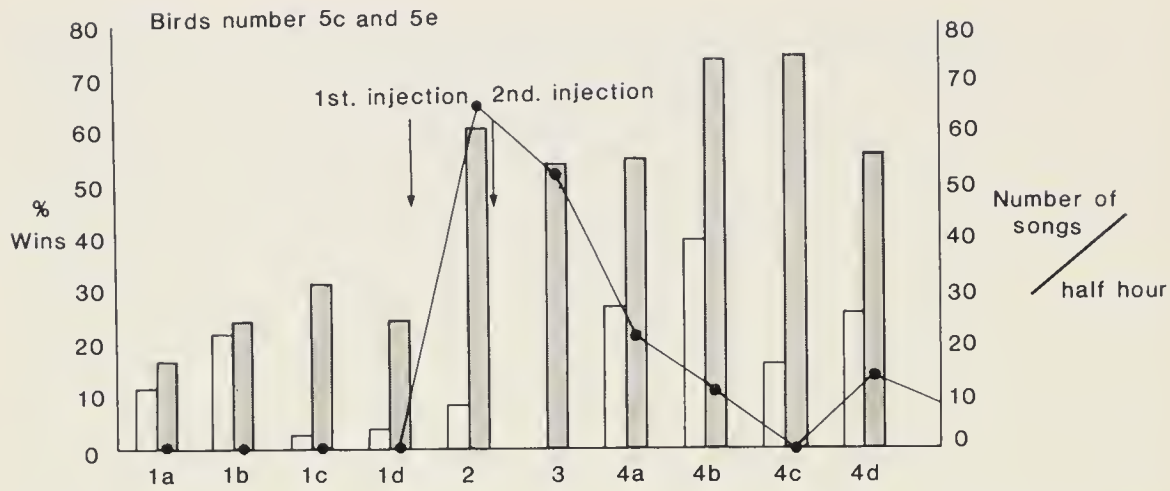

FIG. 3. Relationship of number of songs and number of wins in birds 5c and 5e. Vertical bars represent percentage of wins of experimental bird 5e (gray bars) versus control bird 5c (open bars) at four-day intervals beginning 13 January and ending 21 February. Dots represent mean number of songs sung per half-h by experimental bird 5e during those periods. Abscissa represents observations during periods 1 to 4: Periods 1 and 4 are divided into 4-day intervals. Periods 2 and 3 consist of two 4-day intervals of observation.

gens. Treated birds continued to win encounters, however, suggesting that these wins are the result of experience gained by winning encounters during Periods 2 and 3.

Summary.—Testosterone injections rendered low-ranking birds more aggressive thus increasing the number of wins following injections and effecting some status reversals. Following reversal (Period 4) the newly subordinate birds are conditioned through the experience of repeatedly losing encounters to retain their new status, despite the fact that testosterone titers are no longer high in their opponents.

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Growth characteristics of Wood Ducks from two southeastern breeding locations.—Recently, advances have been made in the application of the Richards sigmoid model to the study of avian growth. These studies (White and Brisbin 1980, Brisbin et al. 1986) have provided a means of evaluating bird growth by making independent estimates of the three major components of the growth process: (1) *size,* or asymptotic limit approached, (2) *rate,* a measure of the total amount of time required for growth to be completed, and (3) *shape,* a quantity which expresses the specific path or trajectory taken by the growth process to approach asymptote within the time constraints of the total growing period. In this reparameterized process error model, these three characteristics are quantified by the parameters W_∞, T, and m, respectively (Brisbin et al. 1986).

Preliminary studies that used these procedures to analyze the growth of waterfowl and other organisms have suggested that, following exposure to a variety of environmental stressors, changes in growth curve shape (m) are more likely to occur than are changes in either size (W_∞) or growth rate (T) (Brisbin et al. 1986). Fendley and Brisbin (1977), however, found that sigmoid growth characteristics of captive-reared Wood Ducks (*Aix sponsa*) also can vary according to the breeding location. In that study, growth rates were found to vary between birds from different locations, but no difference was found in asymptotic sizes. There was also a suggestion of a change in the shapes of the growth curves, as evidenced by a shift in the ages at the point of inflection, although this could not be tested conclusively as analyses in that study were based on the use of the logistic rather than the Richards sigmoid model. (The logistic model is a special case of the Richards model that is obtained by constraining m = 2, and therefore changes in the value of m cannot be detected.)

We report here the use of the reparameterized Richards process error model to analyze the sigmoid growth characteristics of captive-reared Wood Ducks that were collected as

TABLE 1

PROBABILITY LEVELS FOR MULTIVARIATE (MANOVA) AND UNIVARIATE ANALYSES OF ASYMPTOTIC WEIGHT (W_∞), GROWING PERIOD (T), AND CURVE SHAPE (M) FOR RICHARDS SIGMOID MODELS FOR CAPTIVE-REARED WOOD DUCKS FROM TWO BREEDING LOCATIONS (UNDERLININGS EMPHASIZE SIGNIFICANT EFFECTS [$P < 0.05$])

Source of variation	MANOVA	W_∞	T	m
Sex	0.003	<0.001	0.651	0.458
Breeding location	0.003	<0.001	0.626	0.386
Sex × breeding location	0.464	0.221	0.398	0.893

hatching eggs from nest boxes from two breeding locations approximately 220 km apart. Eggs were collected from Clemson, Anderson County, South Carolina (34°41′N, 82°50′W), and Rome, Floyd County, Georgia (34°15′N, 85°10′W). Details concerning the collection of eggs, incubation, hatching, rearing, and weighing of birds used in this study are in Mayack et al. (1981), who report the results of chronic cadmium feeding in combination with two levels of dietary protein (18 and 30%). Data for the Clemson ducklings of the present study were those collected for the control birds used in the study by Mayack et al. (1981). All ducklings were combined in rearing pens and raised under identical conditions.

Growth data for body weights of the ducklings were fit to the Richards process error model defined by the equation:

$$\frac{W_{i+1} - W_i}{t_{i+1} - t_i} = \frac{2(m + 1)}{T(1 - m)}(W_\infty{}^{1-m}W_i{}^m - W_i) + e_i$$

where: W_i is the body weight at time t_i, W_∞ is the asymptotic weight, T is the overall growing time, indicative of growth rate, m is the Richards shape parameter, and e_i is the stochastic error at time t_i.

Further details concerning the derivation of the parameters m and T are provided by Brisbin et al. (1986), and a description of the incorporation of e_i into the model is provided by White and Brisbin (1980).

The three parameters (W_∞, T, and m) were estimated for each duck and then treated as the vector (W_∞, T, m) for multivariate analysis of variance (MANOVA) (Brisbin et al. 1986). For the multivariate analysis of variance, a fixed effect model was used, containing effects for sex, breeding location, and their interaction. Parameter estimation and MANOVA procedures were carried out using procedures NLIN and GLM, respectively, of the Statistical Analysis System (Sas Institute Inc. 1982).

Multivariate analyses revealed that both sex and breeding location significantly affected the growth of the Wood Ducks. The interaction between these two variables failed to show significance in either the MANOVA or univariate cases (Table 1). Univariate analyses indicated that W_∞ was the only growth parameter that differed significantly between the sexes and breeding locations. Male ducks tended to grow to larger asymptotic weights than females, and males and females from Clemson were larger than those from Rome (Table 2).

The pattern of differences in growth between the sexes of Wood Ducks, as reported here, was similar to those reported previously (Brisbin et al. 1986), using these same analytical procedures to study the growth of this species. In each case, the growth of the sexes differed significantly, with males growing to larger asymptotic weights than females. In no case has sex ever interacted significantly with any other primary treatment variable. Thus, with respect

TABLE 2

MEANS OF ASYMPTOTIC WEIGHT (W_∞), LENGTH OF GROWING PERIOD (T), AND CURVE SHAPE (M) FOR RICHARDS SIGMOID MODELS FOR CAPTIVE-REARED WOOD DUCKS FROM TWO BREEDING LOCATIONS

Sex	Breeding location	N[a]	W_∞ (g)	T (days)	m
Male	Clemson, South Carolina	21	520.0 (7.8)[b]	55.4 (10.6)	1.25 (28.2)
	Rome, Georgia	17	469.7 (5.6)	57.8 (12.4)	1.35 (25.7)
Female	Clemson, South Carolina	24	469.7 (10.6)	57.4 (15.8)	1.34 (31.8)
	Rome, Georgia	10	443.6 (4.7)	56.6 (14.2)	1.42 (35.1)

[a] Number of estimates of each parameter determined for individual birds.
[b] Mean (% coefficient of variation).

to growth, Wood Ducks of either sex seem to respond similarly to external stressors and environmental variables such as breeding location.

The lack of significant differences in either overall growing times or growth curve shapes between birds from the two locations (Tables 1 and 2) suggests that although ducklings from the Clemson population tended to add more body weight per day, they still showed the same timing of maximum growth rate (point of inflection of the growth curve) as did birds from the Rome location. At both locations, time of maximum growth (point of inflection) occurred at approximately 19–20 days of age. An average shape parameter of 1.33, pooled for birds of both sexes from both locations, suggests a curve shape intermediate between the Gompertz ($m \rightarrow 1.0$) and logistic ($m = 2.0$) growth models.

With the exception of laying and early incubation, all birds used in this study were produced and raised under identical captive conditions. This strongly suggests that the differences observed in growth asymptote were genetic in nature. Some environmental influence might have taken place, however, if differential habitat quality or stress affected egg quality in the study areas and thus duckling nutrient reserves at hatching (Marcstrom 1966). Localized genetic differences, on the other hand, might be minimized by the relatively short distance between the study sites, and by the fact that Wood Ducks tend to pair on the wintering grounds after which the drake tends to return with the hen to breed in her natal area (Grice and Rogers 1965).

Our finding of no significant differences in either total growing time or shape of the growth curves is in contrast to the earlier findings of Fendley and Brisbin (1977). This suggests that allowing growth curve shape to vary freely may change the conclusions from those which would have been reached by analyses in which curve shape was not allowed to vary (e.g., the monomolecular, logistic, Gompertz, von Bertalanffy).

Finally, and perhaps most significantly of all, is the fact that even when quantified and allowed to vary, growth curve shape in the present study did not differ between treatment groups. In every other study which has used the curve-fitting and analytical procedures described here, curve shape has been the most frequent to differ of all the growth parameters tested (Brisbin et al. 1986). Our findings indicate that there is no intrinsic mathematical artifact that causes such variation in curve shape between treatment groups. Furthermore, the results presented here support the contention (Brisbin et al. 1986) that growth curve shape represents a "first line of defense" by which the growth strategy of an organism may respond to externally imposed environmental stress or perturbation. As all ducklings used in this study grew under identical environmental conditions that were aimed at minimizing stress and optimizing the environmental conditions for growth, we expected that, within

each sex, growth curve shape should not vary between groups from different breeding locations. Under these conditions, however, differences in asymptotic size could still be expressed between the sexes and could be evaluated in a straightforward manner.

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Effect of snow cover on starling activity and foraging patterns.—Winter is often a time of high mortality for temperate bird populations (Dunnett 1956, Gibb 1960). Low food availability may be worsened by periods of prolonged snow cover (Hamilton 1949). Moreover, a bird must be able to acquire more food during the short winter day than at any other time to maintain its body weight; lighter birds suffer significantly higher mortality than their heavier conspecifics (Kendeigh 1934).

TABLE 1

ACTIVITIES AND FOOD SOURCES USED BY FLOCKS OF STARLINGS ON 10 SNOWLESS DAYS AND 10 DAYS OF COMPLETE SNOW COVER

Ground condition	Activity				Food source			
	Foraging	Flying	Loafing	Total	Grasses and lawns	Agri-cultural fields	Human-generated	Fruit trees
Snow-covered	114 (21)[a]	171 (31)	265 (48)	550	16 (14)[b]	4 (4)	88 (77)	5 (4)
Snowless	214 (36)	107 (18)	281 (46)	602	94 (43)	24 (11)	88 (42)	6 (3)

[a] Percent of all flocks.
[b] Percent of foraging flocks.

Many temperate European Starlings (*Sturnus vulgaris*) are able to maintain normal body weight in winter (Dunnett 1956), and populations apparently suffer little mortality even during severe winters (Coulson 1960). Starlings are especially capable of exploiting human-generated foods (e.g., feedlots, handouts) during winter. For example, Hamilton (1949) reported an increased reliance on these food sources by starlings after a single snowfall. Such opportunism might account for the starling's success in winter. Here I describe changes in the activity patterns and food sources used by starlings after a series of snowfalls.

Methods.—I established two circular 300-km^2 study areas in central New Jersey. Franklin, in Middlesex County, was mainly urban-suburban with little agriculture. Adelphia, about 40 km SSE of Franklin in Monmouth County, was predominantly rural-agricultural with large wooded tracts. Roadside censuses were conducted along 50-km established routes in each area. Censuses began within 30 min after sunrise and lasted approximately 3 h. At the start of each census, I recorded temperature, snow depth, and wind velocity. I drove at an average speed of 30 km/h and recorded all starling flocks (one or more birds), using three categories of activity: foraging, flying, and "loafing." The latter category included sitting, preening, and displaying. Censuses were taken both the day before and the day after a snowfall that completely covered the ground (mean snow depth: 10 ± 4 cm; range = 6–20 cm). Snowfalls in central New Jersey are generally widespread. Ten of these paired observations were made between December and April, with not more than one pair per week.

I measured invertebrate density in grasses and grain density in harvested corn and soybean fields (Maccarone 1985). These habitats are used extensively by starlings in central New Jersey (Fischl 1983). In each area, three lawns and three of both types of crop field were sampled every two weeks before the first snow cover in late December. I determined land cover types by physical inspection of 500 random points in each area.

Results.—A total of 550 starling flocks was observed during 10 days of complete snow cover, and 602 flocks were observed on 10 snowless days (square root transformation, $t = 0.69$, df = 18, $P > 0.10$). There was, however, a significant effect of ground cover condition on activity ($\chi^2 = 41.32$, df = 2, $P < 0.001$) (Table 1). A greater proportion of flocks foraged during censuses taken on snowless days than did flocks censused on days of snow cover (Wilcoxon, T = 8, df = 10, $P < 0.05$). There was no difference between ground cover conditions in the proportions of flock flying or loafing.

Food sources used by starlings also differed between days of snow cover and snowless days ($\chi^2 = 43.23$, df = 3, $P < 0.001$) (Table 1). The same number of flocks (88) used human-generated food sources during both ground conditions; however, that number comprised

77% of all foraging flocks (71% of all birds) on snow days but only 42% of all foraging flocks (19% of all birds) on snowless days (Wilcoxin, T = 0, df = 10, $P < 0.001$). The size of flocks using human-generated foods did not differ between snow (7.0 ± 7.0 [SD]) and snowless (6.5 ± 7.3) days.

Flocks foraging on grasses on snowless (17.1 ± 25.6) and snow (5.8 ± 5.3) days did not differ. Those few flocks using grasses during snow days were observed on the leeward side of buildings and windrows. Flocks using fruit-bearing trees were larger on snowless (17.1 ± 13.1) than on snow (3.4 ± 0.9) days ($t = 2.31$, df = 11, $P < 0.05$), while those in crop fields were similar on snow (31.2 ± 11.8) and snowless (31.9 ± 40.2) days.

Mean ambient temperature at the start of censuses taken on snow days was −2.2 ± 2.6°C, and −3.2 ± 2.3°C on snowless days. In neither ground cover condition was ambient temperature correlated with the proportion of all flocks observed foraging, or the proportion of foraging flocks using commensal foods. Mean wind velocity did not differ between snow (16 ± 8 km/h) and snowless (16 ± 10 km/h) days, and it was not correlated with activity or use of food sources in either ground cover condition.

Invertebrates in grasses and grain in harvested crop fields were still abundant by early winter. In December, shortly before the first snowfall, the density of lawn invertebrates (>5 mm long) was 15 ± 31 individuals/m^2. This included mainly beetle larvae and other arthropods. Soybean density was 80 ± 30 soybeans/m^2, and kernel density was 42 ± 48 kernels/m^2. Grasses, soybean fields, and corn fields together accounted for 35% of the combined Franklin and Adelphia surface area and were used by 55% of foraging flocks when the ground was clear. After complete snow cover, only 17% of all foraging flocks used these same substrates.

Discussion.—The sharp decrease in the number of foraging flocks suggests that starlings had a more difficult time finding food after a snowfall. Feeding activity appeared to be somewhat less affected by wind velocity and ambient temperature, neither of which differed with ground cover conditions.

The most apparent change was the twofold increase in the proportion of foraging flocks using human-generated foods. A similar proportionate increase was found by Hamilton (1949). Compared to that study, however, reliance on human-generated foods in the present study was substantially higher on both snowless and snow-covered ground. It is possible that increased urbanization may provide additional opportunities for starlings.

The aggression often observed among foraging birds at human-generated food sources may explain why the number of flocks using these sources did not change after a snowfall, despite an increase in proportionate use. Garbage pails and food scraps are more readily defended than more homogeneously distributed foods, and aggression may limit access (Stokes 1962). Proportionate use of human-generated foods by starlings is highest in winter (Maccarone 1985), and these sources may be defended during this season even when the ground is clear. Many birds that did not compete successfully at dumpsters and feedlots may have loafed (conserving energy while waiting for a better opportunity) or moved elsewhere to forage.

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Agonistic communication among wintering Purple Finches.—Agonistic displays traditionally have been viewed as exchanging information on the motivations and intentions of the signaler (Dawkins and Krebs 1978, but see Hinde 1981). Dawkins and Krebs (1978) argue there is no apparent advantage to an individual involved in a conflict to reveal its intentions or motivations. An individual may benefit most by lying about its intentions in order to deceive its opponent. This has led to the hypothesis that no true information should be communicated by agonistic signals. Other workers have retained a traditional view and argue that agonistic displays do communicate information and that individuals should have the ability to detect lying (Rhijin 1980, Hinde 1981).

Studies of agonistic communication have not provided complete support for either viewpoint. In reanalyzing data from 3 earlier studies, Caryl (1979) concluded there was no evidence that signalers revealed their intentions during agonistic displays. Other recent studies have reached the conclusion that agonistic displays *do* communicate the intentions (Bossema and Burgler 1980, Nelson 1984) or relative fighting abilities (Clutton-Brock and Albon 1979, Evans 1985) of the signaler. This study reports on information transfer during agonistic communication among Purple Finches (*Carpodacus purpureus*) in winter flocks. I describe the agonistic displays of the Purple Finch and the general course of agonistic encounters, and ask the following questions: (1) Do responses to signals vary with the type of display given? (2) Do displays predict the signalers' next acts? (3) Do winners and losers differ in their use of displays?

Methods.—Aggressive encounters were videotaped at a feeder at Elkhart Lake, Sheboygan County, Wisconsin, in January 1985. The Purple Finch is an irregular winter resident at the study site, and the finches came to the feeder in flocks of approximately 10–20 birds. A Panasonic video camera (Model WV-3400) was concealed in an enclosure 3 m from the feeder. All videotaping was done between 07:00 and 11:00 CST. The feeder, stocked with a mixture of thistle and small black sunflower seeds, was 1.5 m off the ground and had a 7 × 25 cm platform from which the finches could feed. The American Goldfinch (*Carduelis tristis*) was the only other species that visited the feeder regularly.

Finches fed on the platform, and aggressive encounters occurred over access to the seeds.

TABLE 1
RESPONSES OF PURPLE FINCHES TO DISPLAY TYPES

Display	Percent of responses					N
	Low Head Forward display	High Head Forward display	Bill display	Bill display with pecking	Retreat	
Low Head Forward	19	45	31	0	5	62
High Head Forward	0	16	68	0	16	56
Bill	0	0	42	10	48	118
Bill display with pecking	0	0	0	29	71	17

Through the use of slow-motion replay, the exact sequence of displays was determined for each encounter. Replays also made it possible to follow each individual throughout an encounter. None of the finches was colorbanded. An individual was considered to have lost an encounter (retreated) if it fled from the feeder or gave a submissive posture. An individual won an encounter if it remained on the feeder while its opponent retreated. Winners of encounters gained or retained access to the feeder. Individuals escalated an encounter if they responded to a display with another display. Encounters involving more than 2 individuals or any interspecific encounters were excluded ($N = 51$). I analyzed 351 encounters.

For each display given, I noted (1) the type of display, (2) the response of the recipient, and (3) the act of the signaler following the recipient's response. Recipients responded to displays either by giving a display, pecking the signaler, or by retreating. Signalers then either displayed, pecked their opponent, retreated, or remained on the feeder while their opponent retreated. For each display type, it was determined how frequently recipients used each response and how frequently each behavior was used by signalers in their next act. All statistical comparisons were done with a G-test.

Results.—I observed 3 types of agonistic display. In the Low Head Forward display the individual is in a horizontal position, with its neck partially extended and bill pointed at the opponent. In the High Head Forward display the finch is in a more upright posture with the neck extended towards its opponent; the bill is often open in a gape. In the Bill display the bird stands vertically, its body extended to its full height, pointing its bill downward at the opponent. The contestants sometimes grab each other's bills and alternate giving the Bill display. Finches may peck their opponents, at times repeatedly, while giving the Bill display. I observed no ritualized submissive posture, although birds did lean away and hop backwards from opponents.

Aggressive encounters were divided into the following categories: (1) Supplanting (7% of all encounters), which occurred when an individual flew directly at a finch on the feeder, and the perched individual fled immediately. The supplanting individual replaced the perched individual on the feeder. No displays were given during these encounters. (2) Single display encounters (70% of all encounters), in which birds directed a display at an opponent who immediately retreated. Most single display encounters were initiated with the Low Head Forward display (62%), with other initiating displays being the High Head Forward (21%), the Bill display (16%), and the Bill display with pecking (1%). (3) Multiple display encounters (23% of all encounters), in which both contestants displayed.

During multiple display encounters, recipients varied their responses to agonistic displays depending on the type of display given by the signaler ($G = 167.4$, df = 12, $P < 0.001$) (Table 1). Three major trends were apparent. First, displays differed in how effective they

TABLE 2

NEXT ACT OF SIGNALERS AFTER GIVING A DISPLAY

Display	Percent of next acts						N
	Low Head Forward display	High Head Forward display	Bill display	Bill display with pecking	Retreat	Win	
Low Head Forward	0	13	43	0	39	5	62
High Head Forward	0	2	46	4	32	16	56
Bill	0	0	17	9	26	48	118
Bill display with pecking	0	0	0	0	29	71	17

were in causing the recipient to flee. The Low Head Forward display was the least likely to be followed by fleeing (least effective), and the Bill display was the most effective. Second, pecking occurred only in response to the Bill display and Bill display with pecking. Thus, as displays became more effective, they also became riskier. When responding with a display, recipients always used a display of equal or higher intensity.

The next act of the signalers depended upon the type of display they had given initially ($G = 87.9$, df = 15, $P < 0.001$) (Table 2). Signalers were more likely to win an encounter after giving the Bill display. Signalers pecked at their opponent in their next act more as signal intensity increased.

Winners and losers varied in the frequency that they used each display. Winners used the Bill display most frequently; losers made greater use of the lower intensity displays ($G = 38.2$, df = 3, $P < 0.001$) (Table 3). Winners and losers also differed in how they escalated encounters. Losers were more likely than winners to escalate an encounter with a display equal in intensity to the preceding display rather than with one of higher intensity (36.4% vs 12.3%); winners were more likely than losers to use a display of higher intensity (87.7% vs 63.6%, $G = 7.7$, df = 1, $P < 0.01$). For example, in response to the High Head Forward display losers used the same display 85.7% of the time, while winners gave the Bill display 92.5% of the time. Losers rarely escalated encounters by using the Bill display.

Discussion.—The high percentage of single display encounters indicates that displays were highly effective in causing the recipient to flee. Each display type, however, had its own

TABLE 3

THE PERCENT EACH DISPLAY WAS USED AMONG ALL DISPLAYS GIVEN BY WINNERS AND LOSERS

Display	Percent use	
	Winners	Losers
Low Head Forward	20	31
High Head Forward	11	37
Bill	61	28
Bill display with pecking	8	5
N	145	108

effectiveness. In multiple display encounters, as displays became more effective, they also became riskier to use because of the increased probability of pecking by the recipient. Finches may have minimized risk by initiating encounters with the Low Head Forward display, the least risky display. If this initial display was ineffective, encounters showed a pattern of escalation with the displays being used becoming both more effective and more risky. Encounters might be viewed as a series of steps in which each contestant decided whether to give a display and escalate the encounter or to retreat, the winner being the finch most willing to risk injury and use the higher intensity displays. Purple Finch conflicts resemble Caryl's (1981) "war of nerves" in which costs (the risk of pecking) mount as the contest proceeds. The differences between winners and losers further support the conclusion that agonistic displays convey information. The way an individual uses displays and escalates an encounter provides information on its willingness to remain in the conflict and its likelihood of winning that encounter.

None of the displays proved to be good predictors of attack (pecking). A similar result led Caryl (1979) to conclude that agonistic displays do not convey the signaler's intentions. This conclusion, however, is based on the assumption that agonistic signals are meant to communicate the intention to attack. In this study agonistic displays are very effective in causing an opponent to flee. It is not surprising that the displays rarely predict attack: one cannot attack an opponent who is not there. My results suggest that agonistic displays convey the signaler's intention to remain in the contest and to risk a possible attack. Signalers may be kept honest in communicating their intentions by the risk of attack (Rhijin 1980).

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Prey robbery by nonbreeding Magnificent Frigatebirds (*Fregata magnificens*).—Age- and sex-related differences have been reported in attack frequencies and success rates for several species of pirating frigatebirds (*Fregata* spp.) (Verner 1965, Diamond 1975, Nelson 1976, Gochfeld and Burger 1981). Here we present data on prey robbery in a nonbreeding population of Magnificent Frigatebirds (*Fregata magnificens*) on Daphne Major Island, Galapagos, Ecuador. Our objectives were to (1) examine host use in relation to host abundance, (2) determine whether differences in frequency and success of piracy existed between age- and sex-classes of frigatebirds, and (3) consider whether aggressive interactions between individual frigatebirds might account for observed patterns of prey robbery.

Methods.—Daphne Major is a sparsely vegetated crater, 120 m high and 32 ha in area, about 8 km north of Santa Cruz Island (Grant et al. 1975). Blue-footed Boobies (*Sula nebouxii*), Masked Boobies (*S. dactylatra*), Red-billed Tropicbirds (*Phaethon aethereus*), and Swallow-tailed Gulls (*Creagrus furcatus*) breed on the island (Table 1). About 46 Magnificent Frigatebirds used the island as a roost but did not breed there. The nearest nesting colony of this species was about 8 km west of Daphne on Seymour Island (Harris 1974).

We watched frigatebirds at 2 sites on the island from 1 February to 18 May 1982. There was no substantial difference in frigatebird or seabird behavior between areas, and data from both sites were combined. Birds were watched on 12 occasions for from 2.5 to 12 h each time (99 h total).

The frigatebird population on Daphne was censused at the roost at 05:45 h before 5 watches. Most frigatebirds remained in the roost until then. Numbers of host species were determined in February 1982 by direct counts of nests (Blue-footed and Masked boobies) and by combining nest counts and visual estimates of population sizes (Red-billed Tropicbirds and Swallow-tailed Gulls).

We defined attempted prey robbery as an interaction in which a frigatebird, alone or as part of a group of attackers, actively pursued to within 5 m of another seabird. For each attack we recorded time, age, and sex of the attacker(s) (male, female, or juvenile as distinguished by plumage characters [Nelson 1976]), host species, occurrence of physical contact, and outcome of attack. We assume that most hosts that were attacked carried food, although we did not determine this directly.

We also noted the age and sex of pairs of frigatebirds involved in any intraspecific aggressive interactions. To examine the effects of aggressive interactions on frigatebird activity patterns we recorded, in two of the watches at 15 min intervals, the number, age, and sex of frigatebirds in the roost and those flying low (<100 m) or high (>150 m) above the island.

We used Chi-square tests, Fisher's Exact Probability tests (FEP), and Binomial tests to analyze the data. Attack and success "rates" are reported as either the percent of the total attacks made by each group or the percent of total successful attacks. The relative abundance of birds in different age- and sex-classes was estimated by mean numbers of each class present in the roost.

Results.—The number of frigatebirds at the roost averaged 46.3 ± 18.5 [SD] (N = 5) and averaged 23% adult males, 69% adult females, and 8% juveniles. The relative proportion of males : females : juveniles observed in the roost remained relatively constant (3:10:1) during the study ($\chi^2 = 2.41$, df = 8, $P = 0.95$). At 06:00, most frigatebirds left the roost and either flew out to sea, presumably to feed, or remained in the vicinity of the island. An average of 20.9 ± 15.6 (N = 96) individuals remained near the island throughout the day.

We observed a total of 435 piratical attacks, most of which (78%) were made on tropicbirds (Table 1). Of the total attacks on all seabirds, 36 (8.3%) were successful. Success rates varied among host species ($\chi^2 = 36.38$, df = 3, $P < 0.01$) (Table 1). Attacks on Swallow-tailed

TABLE 1

PIRATICAL ATTACKS ON SEABIRDS BY THE MAGNIFICENT FRIGATEBIRD ON DAPHNE MAJOR, GALAPAGOS, ECUADOR, 1982

Host species	Estimated number of individuals[a]	Type of attack			% success rate
		Aerial	Nest	Total	
Blue-footed Boobies	876	10 (3)[b]	73 (100)	83 (19)	11
Masked Boobies	696	3 (1)	0	3 (1)	0
Red-billed Tropicbirds	300	338 (93)	0	338 (78)	8
Swallow-tailed Gulls	50	11 (3)	0	11 (3)	22

[a] In local population.
[b] N (% of column total).

Gulls were most productive. Success rates on all other host species were significantly lower and not different from each other ($P > 0.05$).

Aerial attacks (83% of total attacks; 7.5% success rate) occurred when frigatebirds harassed seabirds by diving quickly at the intended victim and chasing it briefly (<5 sec). Successful attacks on tropicbirds occurred only after a frigatebird grabbed a host's tail in its bill for 2–3 sec, but in 35 of the 62 attacks involving tail-grabs, no food was obtained by the frigatebird.

Frigatebirds also attacked Blue-footed Boobies at their nests (17% of total attacks; 11% success rate), primarily by interrupting food transfer between parents and chicks. The success rate of these attacks was the same as for aerial attacks on all species ($\chi^2 = 0.008$, df = 1, $P = 0.94$).

We also observed sequential attacks by different birds on the same host as well as interactions in which several frigatebirds attempted to rob food that had already been obtained from a host by another frigatebird.

We classified 131 attacks (36.2% of the aerial attacks; 31.0% of all attacks) as parts of sequential attacks on single hosts (N = 34). Only 4 attacks at the nest (5.4%) fell in this category. Proportionately more of the sequential attacks occurred in the air than at nests (FEP, $P < 0.01$). Regurgitation rates were similar in singly attacked and sequentially attacked victims (FEP, 10% vs 14%, $P = 0.31$).

In 7 of 21 instances of intraspecific piracy (nest and aerial attacks combined) in which a mean of 3.5 ± 3.2 individuals attempted to gain the original attacker's stolen prey, at least one attacking frigatebird obtained food. The success rate per bird is similar to the overall success rate for interspecific piracy (8.3% vs 7.5%, $\chi^2 = 0.25$, df = 1, $P = 0.88$).

Male frigatebirds attacked seabirds much more frequently (N = 365; 84% of all attacks) than did females (49; 11%) or juveniles (23; 5%). When the relative abundance of different classes of birds was accounted for, we found no effect of age on attack frequency (adult males and females vs juveniles, $\chi^2 = 0.17$, df = 1, $P = 0.26$), but a strong effect of sex (males vs females, $\chi^2 = 100.37$, df = 1, $P < 0.0001$), with proportionately more attacks by adult males than by adult females. There was no difference in the success rates of adult males and females (8.2% vs 6.1%, $\chi^2 = 0.052$, df = 1, $P = 0.82$), nor in the success rates of adults and juveniles (8.0% vs 13.0%, $\chi^2 = 0.22$, df = 1, $P = 0.68$).

Frigatebirds frequently acted aggressively towards each other even when they were not carrying any prey (N = 140). These interactions usually ended with the chased bird leaving the area in which the interaction occurred. Most chases involved 2 males (N = 64; 54% of total) or one male and one female (N = 16; 18% of total). Males chased females in 12 of

16 instances (Binomial test, $P = 0.07$), and they dominated juveniles in 20 out of 21 interactions ($P < 0.01$).

When the number of birds seen high (>150 m) or low in the sky were summed over 2 days, males were seen within 150 m of the surface a greater proportion of times (45% of 267 observations) than were females (4% of 149 observations) ($\chi^2 = 80.46$, df = 1, $P < 0.001$) or juveniles (16% of 31 observations; $\chi^2 = 8.11$, df = 1, $P < 0.01$). Most piratic attacks were initiated within 100 m of the island surface.

Discussion.—Tropicbirds may have been attacked more frequently than boobies because their smaller bodies and long tails were more easily grabbed during aerial attacks by frigatebirds than were the larger and more compact boobies.

Although Gochfeld and Burger (1981) reported that, overall, pirating adult Magnificent Frigatebirds obtained more food than pirating juveniles, when they calculated success on a per attack basis, adults and juveniles were equally successful. Burger et al. (1980) and Verbeek (1977) also reported a lack of age effects on piracy success rates in *Larus* gulls.

Gochfeld and Burger (1981) also noted male-biased attack rates by Magnificent Frigatebirds. They suggested the bias results because males are more common at nonbreeding sites as they provide only limited care and may leave breeding colonies more quickly than females. This hypothesis does not explain the bias in male frigatebird piracy we observed, as females were more abundant than males on Daphne. Attack rates could simply reflect differences in diurnal activity patterns of male, female, and juvenile frigatebirds. Roost and sky counts, however, indicated that a mean of 7 ± 3.3 males and 14 ± 10.5 females and juveniles (grouped to reflect classes of frigatebirds with high and low attack rates, respectively) were near or on the island during the day. When compared with mean roost counts, these values showed no evidence of a disproportionate number of males being present in the vicinity of the island. Alternatively, aggressive interactions between conspecifics may determine differences in attack rates. Male dominance may limit the opportunity that females and juveniles have to rob other seabirds. Adult males may dominate juveniles simply because of their greater experience, and they may dominate adult females because of their lower wing-loading (cf. Harrington et al. 1972). As Andersson and Norberg (1981) have shown that maneuverability in birds is negatively correlated with wing-loading, males, which have 12% lower wing-loading than females, may be more agile, and this could give them an advantage in aggressive interactions where maneuverability is important.

Our results indicate that behavioral dominance may provide an important alternative to frequency-dependence (Brockman and Barnard 1979) as the process leading to intraspecific specialization of piracy in Magnificent Frigatebirds.

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The nest, eggs, and young of the White-whiskered Spinetail (*Synallaxis* [*Poecilurus*] *candei*).—Ovenbirds (Furnariidae) show a remarkable diversity of nest types, and the structure and location of the nest are of taxonomic importance in this New World family (Vaurie 1980). The nest structure of *Synallaxis candei* is of particular interest because a previous account apparently is in error. The only information available to Vaurie (1980) came from a nest from Colombia described by C. J. Marinkelle, who wrote that the nest of *S. candei* is ". . . made of grass and fine twigs, with side entrance, in (a) natural cavity of (a) rotten tree at ground level" (p. 87). Vaurie was hesitant to accept such information, as the nest structure of *Synallaxis* is remarkably constant, and no species had ever been reported building a nest within a tree cavity. Nevertheless, he surmised that ". . . it is possible that this nest is an exception without precedent in the normal location of the nest in this genus" (p. 87). More recently Serna (1984) made a brief account of a nest from northern Colombia. That nest contained 2 eggs, was placed 1 m above the ground in an orange tree, was very large, and was made from twigs. We know of no other report of the nest of this species.

Further interest in the nest structure and nesting habits of *S. candei* stems from the fact that there has been uncertainty about the taxonomic affinities of this species. Todd (1917) proposed the monotypic genus *Poecilurus* for *candei*, and later authors (Peters 1951) included *kollari* and *scutatus* in *Poecilurus*. More recent reviews of furnariids (Vaurie 1971, 1980) include the genus within *Synallaxis*. Vuillemier has further suggested that all 3 species could be considered allospecies of a single superspecies (Vaurie 1980:120). *Poecilurus*, however, is still accepted in some recent works (e.g., Meyer de Schauensee and Phelps 1978). The purpose of this note is to document fully the nest of *S. candei* in an attempt to provide further information on its taxonomic relationships. In addition, we provide brief information on the eggs and young of this species, which may help in further establishing its affinities within the ovenbirds.

S. candei is chiefly a bird of arid regions (thornscrub) of coastal northwestern Venezuela

and northern Colombia. We made our observations in the Paraguaná Peninsula (Falcon State), on the western coast of northern Venezuela, during 5 visits between October and December 1984. Long-term average precipitation in the area is about 450 mm, most of which falls between October and early January; mean annual temperature is approximately 28°C. The tree layer reaches 5–6 m and is a mixture of cacti, evergreen, and deciduous species, and has an understory largely dominated by the cactus *Opuntia wentiana.*

S. candei searches slowly and gleans insects and other arthropods from the ground and bark surfaces, usually below 2 m. Both sexes sing, and, like many other desert insectivores (Immelmann 1963), they retain their territories and remain paired outside the breeding season, which is mainly coincident with rainy periods (Bosque 1984). Both sexes participate in intraspecific territorial defense.

We inspected 4 nests that had eggs or young, as well as 10 nests that were not being used during our visits. The nest of *S. candei* is a bulky structure composed chiefly of dry spinescent or thorny twigs and sticks. As in all other nests of *Synallaxis,* it consists of two parts: a roughly globular egg chamber, and an entrance tube or tunnel that leads laterally into the egg chamber. In addition, large quantities of bark, sticks, and twigs are added over and around the basic structure until it is surrounded completely by a broad shell, giving the nest the appearance of a somewhat shapeless structure. Inner diameter of the egg chamber is 10–13 cm, with walls constructed entirely of interlaced twigs, most of which are thorny (e.g., *Prosopis juliflora, Pitecellobium dulce, Acacia macracantha, Cercidium praecox, Lycium nodosum, Randia gaumeri, Castela erecta, Croton flavens*). The bottom of the egg chamber is usually lined with the green pubescent leaves of *C. flavens.* If those are not available, the nonpubescent leaves of *C. praecox* are readily used. The use of green pubescent leaves for lining the egg chamber is also found in other *Synallaxis* (Skutch 1969, Vaurie 1980). The entrance tunnel is constructed in a similar manner to the egg chamber, but with finer (about 2–4 mm diameter) and shorter (5–12 cm) twigs. If available, the preferred material for the entrance tube is thin twigs of *L. nodosum.* The entrance hole sometimes opens into the center of a chimney-like circular rim, made of thorns of the cactus *Ritterocereus griseus,* or of finer thorny twigs of the same plant species that was used elsewhere in the structure. The entrance tube is often slightly curved, either sideways or upward at its free end, and it most commonly opens toward the upper distal end of the surrounding shell. It typically measures about 30 cm in length and has an internal diameter of about 5 to 6 cm. The egg chamber and the entrance tunnel are covered by a thick thatch of coarser and larger sticks, twigs, and pieces of bark of the same plant species used in the rest of the structure. Pieces in the thatching are piled up rather than carefully interlaced as they are in the main structure. The thatching extends laterally around the nest proper, completely surrounding it, except for the entrance hole, and forming a broad platform around which the birds can walk. Frequently, as in other *Synallaxis,* pieces of shed lizard or snake skin are added to the nest structure or the chamber lining.

Maximum external dimensions of 2 nests were 70 and 75 cm along the long axis, 35 and 48 cm along the short axis, and 30 and 35 cm deep across the egg chamber. Nests were most frequently placed on thorny shrubs (*P. juliflora, C. praecox, C. erecta*) that provided a horizontal supporting substrate. Nest height above the ground for 6 nests was 1.3–2.5 m. Birds were quite wary around the nest, and we did not observe nest construction.

Nests were used for renesting in the same season. A pair that successfully fledged 3 nestlings around 19 December had a clutch of 4 eggs on 31 December in the same nest. One parent attended the fledglings, which still begged for food, while the second incubated the eggs.

The oblong eggs have a smooth, nonglossy shell with the long axis averaging 20.0 ± 0.7 mm [SD] (N = 7) and the short axis 15.9 ± 0.5 mm (N = 7). Average egg weight, measured to the nearest 0.2 g, was 2.5 ± 0.1 g (N = 7). Egg color varied from a rich turquoise blue

to a pale or light niagara green of Ridgway's (1912) color chart. Clutch size in Paraguaná was 3–4 eggs.

One- or two-day-old nestlings have orange flesh-colored skin and legs. Down is grayish and sparse and concentrated mostly on the head, back, and wings. The bill is yellow but white at the gape, the lining of the mouth is yellow and the inner throat is red, the nails are whitish. The eyes were closed and no egg-tooth was present. Older nestlings and newly fledged birds resemble adults; however, the belly is more extensively white in young birds than in adults. Weights of 3 well-feathered nestlings (16.5, 17.0, and 17.0 g), were higher than those of 2 adult males (14.5 and 16.0 g) collected in the dry season.

The nest of *S. candei* most strongly resembles that of the Rufous-breasted Spinetail (*S. erythrothorax*) of Middle America (Skutch 1969). In both species there is a shell or platform surrounding the entrance-way, and in both the entrance opening is in the center of a circular pile of thorny twigs that is raised above the platform. According to Vaurie (1980), an entrance platform has been reported in no other *Synallaxis* except *S. erythrothorax.*

Our description of the nest of *S. candei* confirms that it is typical of *Synallaxis,* as originally suspected by Vaurie, and is in agreement with his contention that *Poecilurus* should be included in the former genus. To the best of our knowledge, there are no published descriptions of the nests of *kollari* and *scutatus,* the other 2 species included by Peters (1951) in *Poecilurus.* Descriptions of the nests of these 2 species would help in establishing the taxonomic affinities of this group within the furnariids.

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Reproduction and molt in the Burrowing Parrot.—The Burrowing Parrot (*Cyanoliseus patagonus*) has one of the southernmost ranges of neotropical parrots. In Argentina, it occurs from the arid Andean slopes in the northwest (24°S) to the Patagonian steppe in the south (46°S) (Forshaw 1978). The parrot, which nests colonially in burrows dug into cliff faces, is shot as an agricultural pest and has recently been exported in large numbers for the pet trade, causing local declines in its population (Ridgely 1980). Here, we report on the cycle of wild Burrowing Parrots in terms of changes in body weight, fat deposits, gonadal condition, and molt.

Study area and methods.—The study area was between 33° and 33°30′S and 66° and 67°W in the plains near the Sierras de San Luis, San Luis province, central Argentina. The predominant vegetation is an open dry woodland savanna mixed with grasslands. Dominant tree species include *Geoffroea decorticans, Prosopis caldenia, P. chilensis,* and *P. flexuosa,* all of whose fruits are eaten by Burrowing Parrots.

Annual rainfall, which is concentrated in the summer (November–April), averages 69.5 cm. Mean annual temperature is 17°C (Instituto Nacional de Tecnología Agropecuaria, Villa Mercedes Experimental Station, 30 km east of the study area).

We obtained parrots from farmers involved in control campaigns, as the Burrowing Parrot is considered a pest by local authorities. We obtained 7–35 parrots monthly from September 1978 to August 1979, with the exception of December 1978, when only two birds were obtained. Birds came from Paso de las Carretas, near Eleodoro Lobos, except in May, June, and July 1979, when all but a few parrots had left the area, and the sample was completed with birds obtained in Alto Pencoso, about 100 km west. In November 1983 we collected an additional 14 birds at Paso de las Carretas.

Birds were frozen within 10 h of being shot. The delay between collection and processing may have altered some variables, especially body weight (Clark 1979), but the source of error was constant during the study period.

All specimens collected belonged to the *patagonus* race (Forshaw 1978). We recognized two age classes: juvenile (=first year birds) and adult (second year and older birds). Juveniles had a horn colored patch on the mandible (Forshaw 1978) and the presence of the Bursa of Fabricius. Their ability to breed is unknown.

Each specimen was weighed (with and without crop contents) and examined for molt. The amount of visceral and subcutaneous fat was assessed visually on a scale of 0 (no fat) to 2 (very fatty). Primaries and secondaries were counted from the carpal joint outwards. Tail feathers were counted from innermost out. Molt in remiges was scored as follows: old feathers, 0; empty sockets of pin feather, 1; feather up to one-third grown, 2; feather up to two-thirds grown, 3; feather nearly full-grown, 4; new full-growth feather, 5. Molt scores were used to plot the progression of primary molt.

Testes were weighed and measured. Ovaries were weighed and the follicles over 1 mm measured. We assumed that (combined) testes weight indicated spermatogenic condition, considering the marked seasonal contrasts registered (cf. Smith and Brereton 1976 and Pohl-Apel et al. 1982). But such conclusions are tentative until histological information is obtained.

Results.—The breeding season begins in September, when the parrots return to nesting colonies. Egg laying starts in November and continues until December. The chicks fledge from the burrow from late December to early February. Fledglings begin to leave the nest area in late January, and remain in the neighborhood dependent upon adults until the end of April. In May, most parrots disperse, but if local resources, such as unplowed crop stubble,

are abundant, at least some birds may remain in the area. In all samples, the sex ratio did not differ significantly from 1:1.

The mean body weight of adult parrots was 270 g. We recorded statistically significant variations in body weight during the year, with one peak in winter (March–June) and another in late spring (November–December), and minima in summer (January) and at the end of the dry season (September–October). Males were usually heavier than females, except in November–December, when females were slightly heavier than males. Juveniles of both sexes were lighter than females. The yearly pattern of fat deposits was irregular, with a higher proportion of very fatty individuals in late winter (July–August) and late spring (November–December). We did not find differences in fat deposits between sexes except in November–December, when fatty females were more common than fatty males (9 of 15 females vs 3 of 14 males, G-test, $P < 0.05$). We found no correspondence between individual fat deposit categories and body weight (Kruskal and Wallis test, $P > 0.05$), possibly due to the subjective nature of the fat deposit index.

Testes enlarged 15 fold from $\bar{x} = 19 \pm 9.5$ mg [SD] (N= 6) in August to 292 ± 100.1 mg (N = 13) in November and then declined rapidly. Changes in ovary weight and size followed a temporal pattern similar to that of the testes. We found eggs in oviducts in November through January. In November 1983 the mean ovary weight in a sample of 13 females was 604 ± 149 mg [SE] (compared with 430 ± 60 mg in 1978), and 4 of the females had eggs in the oviduct.

Replacement of primaries by Burrowing Parrots tends to begin with P6 and works towards P1 and P10, a replacement pattern common in parrots (Stresemann and Stresemann 1966). Primary molt started in November in both 1978 and 1983, and it was complete in most individuals by July. The individual primary molt period has been estimated as 8 months. There is no clear sequence in the replacement of secondaries, also typical in parrots (Stresemann and Stresemann 1966). Secondary molt starts in January and continues throughout August.

The molt of rectrices tends to start symmetrically in T1, followed by T5, T6, and, finally, T2 to T4. This pattern differs from the irregular molt found in most parrots (Forshaw 1978), and the strict centrifugal replacement found in the Budgerigar (*Melopsittacus undulatus*) (Wyndham 1981). Individuals molting rectrices were found in all months, although the period of greatest activity was February through May. We recorded asymmetric molt in 3 of 42 first year specimens, which appeared to represent replacement of lost feathers.

All females collected with eggs in the oviduct (4 in November 1983, 1 in December 1978, 2 in January 1979) were molting; however, as the intensity of molt increased, the proportion of birds in full reproductive condition decreased.

Crop contents indicated predominance of seeds from cultivated crops and wild plants in winter, but fruits from dominant trees became important in summer. Fruit comprised (in percentage of total volume) 2% of crop contents in November–December, 74% in January, 25% in February, 35% in March, and 8% in April (unpubl. data).

Discussion.—The annual cycle of the Burrowing Parrot is typical of seasonally breeding birds in temperate regions (Murton and Westwood 1977, Clark 1979). Molt follows breeding, but there is a partial overlap, which may be related to a reduction in the reproductive costs associated with the use of cavities for nesting (Foster 1975).

The Burrowing Parrot's gonadal and molt cycle are very similar to that of the Eastern Rosella (*Platycercus eximius*), which inhabits more mesic woodland savannas in Australia at about the same latitude (Smith and Brereton 1976, Wyndham et al. 1983), and contrasts with the irregular and opportunistic variations exhibited by the Budgerigar in arid regions of Australia (Pohl-Apel et al. 1982).

We think that the availability of tree fruits as food for the young may be an important

factor influencing the regularity in breeding and molt in the Burrowing Parrot. Fruits are significant items in the parrot's diet during the breeding season (Forshaw 1978, this paper). Furthermore, tree fruit production is more regular than grass seed production in arid environments, as woody plants are less dependent on the irregular rains due to their capability of obtaining water from deeper soil levels (Walker and Noy-Meir 1982).

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Extrapair feeding in Pied-billed Grebes.—Two forms of cooperative rearing through feeding of chicks have been reported for grebes. These are (1) young from first broods feeding siblings from a second brood (Cramp and Simmons 1977) and (2) adults, other than pair members, feeding chicks from a single brood (Lane 1978, Forbes 1985). This latter form has been termed extrapair feeding (Forbes 1985).

On 19 June 1982, I observed 3 adult Pied-billed Grebes (*Podilymbus podiceps*) feeding 5

chicks. All 3 adults were in breeding plumage. Sex of the paired birds was determined by relative body and bill size (Palmer 1962), but the sex of the third adult was not known. Hereafter, I shall refer to the 3 adults as either the male, the female, or the extra adult.

From 17:05 to 19:55, I was in a floating blind (cf. Nuechterlein 1981) in a freshwater impoundment of the Chignecto National Wildlife Area near Amherst (45°50′N, 64°12′W), Novia Scotia. I determined that 7 young had hatched earlier that month from a nest found nearby (<30 m) in a stand of cattail (*Typha* sp.).

At 17:15, I sighted 5 chicks, <10 days old, being fed by the male and the female. The brood moved to within 15–20 m of the blind. Adults surfaced primarily (16 of 22 dives) with 4–8 cm long sticklebacks (*Pungitius pungitius*). At 17:30, another adult moved to within 5 m of the brood and began foraging. I determined from the positions of the adults that all 3 adults were foraging and feeding the chicks. The extra adult fed at least 2 fish to the chick(s).

Foraging soon ceased, and all 3 adults loafed among the 5 chicks. The female swam away followed by all 5 young, which apparently responded to her neck-erect posture or her soft, grunting (Palmer 1962), vocalizations. Meanwhile, the male swam at the extra bird in an exaggerated neck-lowered posture similar to the threat postures of Horned Grebes (*Podiceps auritus*) (Storer 1969). The male and the extra bird then faced off (<1 m apart), with their necks lowered and s-shaped and their cheeks swollen. Both birds engaged in an intense binocular stare for over 20 s. After a brief "circle display" (Palmer 1962) with little pivoting by the birds, the male lunged at the extra adult; despite bill fencing, no nape grasp (McAllister and Storer 1963) resulted. Subsequently, the male drove away the extra adult through a series of flapping chases and returned to the female and her brood. I suggest that all chicks were siblings because they remained together throughout the entire observation period, and because they all responded to the supposed brooding call (Palmer 1962) of the female. Adoption in this solitary grebe should occur rarely. No other extra adults appeared near the brood that evening.

Infrequent feeding by extra adults (one occurrence out of 55 h of observation) should not be considered "helping" (sensu Emlen 1978) as benefit to the brood was trivial. If extra adults are not tolerated (Forbes 1985, this study), then benefits to the proposed helper are also questionable. Forbes (1985) reported males as extra adults during all 3 extrapair feedings in Western Grebes (*Aechmophorus occidentalis*), and he suggested that those males were attempting to procure mates. Support for courtship as a function of extrapair feeding comes from the following 3 lines of evidence: (1) extra males passed food directly to females, (2) paired males were aggressive to extra males (Forbes 1985), and (3) many species of grebes double-brood (Cramp and Simmons 1977). In this report, however, the extra adult passed food directly to the chick(s).

Perhaps extrapair feeding is simply a demand behavior that may be maladaptive given potentially injurious interactions with paired birds or loss of investment to unrelated young. I have twice seen adult Pied-billed Grebes pass prey to coot (*Fulica americana*) chicks. Obviously, such misdirected feeding is not beneficial to the grebe. The persistence of such behavior should be related to the costs associated with it. For example, extrapair feeding may occur more often in colonial grebes (e.g., *Podiceps nigricollis*) (Cramp and Simmons 1977) because identity of chicks can be frequently, albeit temporarily, uncertain. For grebes that practice obligate (e.g., *Podiceps cristatus*) (Cramp and Simmons 1977) or facultative (e.g., *P. podiceps*) (pers. obs.) brood division, extrapair feeding may entail only minor risks whenever there is only one attendant parent. Extrapair feedings involving only 2 adults (i.e., 1 parent) should be more frequent and more persistent. Such encounters have not been reported, probably because they are less obvious.

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Foraging, scavenging, and other behavior of swallows on the ground.—Swallows are aerial foragers that occasionally take prey from on the ground. To our knowledge, 6 species of swallows have been reported feeding on the ground in North America (Barn Swallows [*Hirundo rustica*], Bent 1942, Jackson and Weber 1975, Weber 1980; Cliff Swallows [*H. pyrrhonota*], Bank Swallows [*Riparia riparia*], Jackson and Weber 1975, Weber 1980; Tree Swallows [*Tachycineta bicolor*], Bent 1942, Erskine 1984; Purple Martins [*Progne subis*], Bent 1942; Northern Rough-winged Swallows [*Stelgidopteryx serripennis*], Wolinski 1980, Sealy 1982). Also, Erskine (1984) documented what he believed was ground foraging by Violet-green Swallows (*T. thalassina*). All of these sightings were isolated accounts that, for the most part, involved relatively few individuals. The importance and nature of this foraging behavior is poorly understood. We report ground foraging in 3 species of swallows in Manitoba, including large numbers of migrating Tree Swallows, and describe scavenging from artificial food patches and other nonforaging behavior of swallows that occurred on the ground.

Methods.—We observed swallows on the ground near the southern shore of Lake Manitoba and northern edge of Delta Marsh, Manitoba. From mid-July to late August 1985, several thousand migrating Tree and Bank swallows staged here. About 25 pairs of Barn Swallows nested on the study site, and approximately 100 Cliff Swallows were present in August.

We observed the swallows opportunistically from distances of 10–50 m. Upon encoun-

tering them on the ground we determined the species composition of the flock and estimated the number of individuals in it. Flocks seldom remained intact for more than a few minutes. Tree Swallows were classed as adults or subadults; second-year females and hatching-year birds were not distinguished (see Hussell 1983).

The tendency for swallows to scavenge prey was tested using insects (chiefly midges [*Chironomidae*] with some moths [*Noctuidae*]) that we collected with an ultraviolet light trap and froze. We created food patches by placing several hundred thawed insects on the ground within an area of 0.25 m^2. Also, we created a strand line of dead insects 10 m long and 1.5 m from the waterline of Lake Manitoba. Natural densities of arthropods along roadways were measured by counting within randomly placed quadrats. Weather data were obtained from the Environment Canada Meteorological Station located on the study area.

Observations.—Between 13 July and 22 August we observed 21 flocks of swallows for a total of 15 h. Swallows used 2 areas regularly: a smooth dirt roadway (Site 1) and a dirt and gravel roadway and adjacent mowed grass (Site 2, grass height approximately 5 cm). At both sites, swallows roosted diurnally on overhead wires, on rooftops, and in willows (*Salix interior*).

From 13 to 22 July, 6 observations were made of Tree Swallow flocks on the ground. Flocks were composed of 36 ± 29% adults [SD] (N = 17 counts) and the mean flock size was 48 ± 17 individuals (N = 17 counts).

In this area, massive emergences of chironomids occur frequently throughout the summer (Busby and Sealy 1979, Briskie 1985). Occasionally in 1985, large numbers of chironomids were grounded, apparently due to cool overnight temperatures (average minimum daily temperature for July was 10.8°C). On two such occasions (20 and 21 July) we observed flocks of Tree Swallows feeding on chironomids on the ground (Table 1). Some individuals also picked up and dropped leaves, twigs, grass, or pebbles. Individuals remained on the ground for several minutes at a time. Such foraging activity, however, was interrupted frequently by brief, but sudden flights of the flock. The chironomid emergence of 26 July was followed by warmer overnight temperatures, and the density of chironomids on the ground decreased. No swallows were observed foraging on the ground in this case (Table 1).

Tree and Barn swallows also scavenged dead chironomids from food patches. Only one individual fed from a patch at one time, and Tree Swallows were displaced by conspecifics when feeding in patches on 3 occasions. Bank Swallows did not take food items, although they walked through patches several times and picked up grass from amongst the dead insects.

Barn, Tree, and Cliff swallows scavenged dead chironomids from the strand line on cool mornings (Table 1). They usually landed a few cm from the strand line where they picked up and ingested insects. Birds fed at the strand line until they were disturbed by two Ring-billed Gulls (*Larus delawarensis*) that also fed on the chironomids.

From 23 July to 14 August, 7 observations were made of mixed-species swallow flocks on the ground. The mean flock size was 225 ± 168 individuals (N = 17 counts) and compositions ranged from primarily Tree Swallows in late July to primarily Bank Swallows in mid-August. These flocks, together with the four monospecific Tree Swallow flocks observed from 13 to 22 July, involved individuals engaged in a variety of behavioral patterns. Some activity appeared to be related to maintenance. Sunning postures involving lateral tilting (see Barlow et al. 1963) were assumed by Tree, Bank, and Cliff swallows. Bank Swallows dust bathed, and all species preened when on the ground. The most common behavior observed, however, was the repetitive picking up and dropping of pebbles, grass, leaves, and twigs. Individuals picked up and dropped items as many as 17 consecutive times before turning to other objects. Dried blades of grass were often picked up and carried 5–6 m before being dropped and picked up again. All species and age classes participated in this

TABLE 1

SUMMARY OF RESPONSES OF SWALLOWS TO CHIRONOMIDS OCCURRING ON THE GROUND IN NATURAL CONCENTRATIONS AND IN ARTIFICIAL FOOD PATCHES AND STRAND LINES, 19 JULY TO 1 AUGUST 1985

Date[a]	Time	Site[b]	Overnight min. temp (°C)	Temp. at start of observations (°C)	Flock composition[c]	Chironomid/m[d]	Aerial insects	Ground foraging
July 19	09:00	2	10.0	15.0	37 TRSW	Chironomid patch[d]	Yes	Yes
20	08:00	1	7.5		90 TRSW	47 ± 51 (N = 20)	No	Yes
						5.2 ± 3.6 (N = 10)		
21	08:00	1	8.0		105 TRSW	14 ± 10 (N = 10)	No	Yes
						2.7 ± 3.8 (N = 20)	No	Yes
21	14:00	1	8.0	20.5	100 TRSW	Chironomid patch	Yes	Yes
24	10:00	2	14.0		80 TRSW, 70 BKSW	Chironomid patch	Yes	Yes
26	08:00	1	12.5		none	0.5 ± 1.4 (N = 15)	Yes	No
31	08:00	Beach	7.5	16	none	Strand line	Yes	No
August 1	06:30	Beach	7.5	8.5	8 BASW, 4 TRSW, 1 CLSW	Strand line	No	Yes

[a] Overnight chironomid emergences occurred on 18–19 and 25–26 July.
[b] Site 1 = smooth dirt roadway; Site 2 = dirt and gravel roadway and adjacent mowed grass; Beach = shore of Lake Manitoba.
[c] TRSW = Tree Swallow; BKSW = Bank Swallow; BASW = Barn Swallow; CLSW = Cliff Swallow.
[d] In patches chironomid densities were several hundred per m^2. Strand line was 10–15 chironomids thick and 10 m long. Densities given for 20 and 21 July are listed for shaded and unshaded regions of driveway; density for 26 July is for shaded driveway.

behavior, which occurred on grass and dirt substrates and continued in one instance for at least 35 min.

Intra- and interspecific aggressive interactions were observed frequently in mixed and monospecific flocks of swallows on the ground. These interactions usually involved displacements and threats with the opened bill. Mountings, usually lasting less than 5 sec and resembling copulation attempts, were observed amongst Tree Swallows. In 75 min of observation of 2 Tree Swallow flocks and one mixed flock, we recorded 33 mountings of subadults by adults, 6 mountings of adults by other adults, and 7 mountings of subadults by subadults.

Discussion.—Locally abundant food on the ground apparently was created in July 1985 by the massive evening emergences of chironomids followed by cool overnight temperatures. Weber (1980) observed Bank, Barn, and Cliff swallows feeding on mayflies that had settled in large numbers on pavement in Alabama. His observations also were made during early morning in late July but, unlike in our study, he noted that mayflies also swarmed over grass and were thus available as aerial prey. Weber also noted that swallows handled these large insects with difficulty. We found that swallows experienced similar difficulties handling noctuid moths. Although lepidopteran larvae are sometimes taken, they are generally unimportant in the diet of swallows (Bent 1942).

Tree, Barn, and Violet-green swallows occasionally land on beaches during migration (Bent 1942, Gullion 1947, Kilham 1980). Apart from providing rest sites, beaches can provide temporarily abundant food. Wolinski (1980) observed Northern Rough-winged Swallows landing on a lakeshore to feed on fly larvae on dead fish. Sealy (1982) saw this species scavenging dead midges that had washed up on the shore of our study site. Erskine (1984) reported 15 Tree Swallows apparently foraging among decaying vegetation at the strand line of a lakeshore. Slud (1964) reported Gray-breasted Martins (*P. chalybea*) foraging on a seashore in Costa Rica.

Wolinski (1980) and Sealy (1982) attributed ground foraging by Northern Rough-winged Swallows to opportunistic use of a temporarily available, abundant food supply. Erskine (1984) noted that Tree and Violet-green swallows apparently foraged on the ground when insects in the air were scarce. He hypothesized that Tree and Violet-green swallows return earlier in the spring than do other swallows in North America, possibly because they winter north of the Mexico-U.S. border. Thus they spend more time in cooler climates and may benefit the most by exploiting several sources of food. Tree Swallows exhibit greater plasticity in their diet than other North American swallows and have been known to eat seeds and fruits during cool weather (Bent 1942). Interestingly, only Tree Swallows readily foraged and scavenged on the ground in our study area. The apparent absence of this behavior in Bank Swallows circumstantially supports Erskine's hypothesis. However, this requires further study since we also observed ground foraging and scavenging in Barn and Cliff swallows. Also, Weber (1980) saw Bank Swallows taking mayflies on the ground, and this species has been observed taking maggots from on the ground in England (Clegg 1977).

Erskine (1984) suggested that observations of foraging by swallows in early spring or during cold weather would probably provide more records of ground foraging. Our observations suggest that ground foraging also occurs during the postbreeding period, possibly in response to diurnal temperature changes as well as periods of sustained inclement weather. Brown (1976) noted that Purple Martins in Texas cannot forage for aerial prey when temperatures are below 6°C. Ricklefs (1971) noted that the foraging rates of adult Mangrove Swallows (*T. albilinea*) were sensitive to temperature and that foraging activity increased shortly after dawn and before dusk.

The repetitive picking up and dropping of inedible objects has been observed in young Bank, Tree, and Cliff swallows (Bent 1942). Weber (1980) noted that Bank Swallows often

pecked at cigarette butts and feathers and suggested that juveniles may not discriminate consistently between food and nonfood items. Chapman (in Bent 1942) suggested that when young Bank Swallows picked up bits of dried grass they prematurely exhibited nest-building instincts. Bank Swallows occasionally, and Cliff and Barn swallows regularly, gather nest material from the ground (Bent 1942, Peart 1976). Our observations reveal that adult and young swallows exhibit this behavior. Ashmole and Tovar (1968), Dunn (1972), and Feare (1975) observed juvenile terns picking up inedible objects from the sea surface. These authors considered such "playing" to be part of learning to forage.

Aggressive interactions have been reported amongst breeding (Emlen 1952, Harris 1979, Butler 1982) and nonbreeding (Bent 1942, Barlow et al. 1963) swallows on the ground. We could not be certain whether the mountings we observed were primarily copulation attempts or acts of aggression or dominance (see D'Agostino et al. 1982). Female Cliff Swallows are susceptible to "rape" attempts when they are gathering mud for their nests (Emlen 1952, Butler 1982). Hoogland and Sherman (1976) also found that male Bank Swallows attempted extrapair copulations on the ground. Brewster (in Bent 1942) described attempted copulations amongst young Cliff, Tree, and Bank swallows that were on the ground picking up and dropping plant material. Chapman (in Bent 1942) similarly observed young Bank Swallows mounting and ascribed this behavior to procreative instincts. Barlow et al. (1963) reported mounting attempts of nonbreeding Cliff Swallows that were sunning on the ground. Emlen (1952) described aggressive interactions amongst Cliff Swallows that resembled brief and incomplete copulations. In our study, most mountings were by adults on subadults. Many of the subadult Tree Swallows could have been second-year females which, when perched on the ground, resembled birds in a soliciting posture. This may have released a stereotyped mounting behavior in adult males similar to that described by Barlow et al. (1963).

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December records of seabirds off North Carolina.—Little published information is available concerning offshore winter seabird fauna of the southeastern United States. The only overview of the local seasonal variation in seabirds is that by Lee and Booth (1979). Their summaries were based mostly on North Carolina field studies done from late spring through early fall, and provide little new information on the winter distribution of marine birds. Clapp et al. (1982, 1983) compiled records of all marine birds for the southeastern States, but offshore information was generally unavailable for the winter. During the last few winters I conducted 11 offshore survey trips into shelf and shelf-edge waters off North Carolina during December. All trips departed from Oregon Inlet, North Carolina (29 December 1977; 5 and 30 December 1978; 3 and 28 December 1982; 12, 20, 28, and 29 December 1984; 5 and 22 December 1985). Survey routes typically extended 35 to 55 miles offshore, transecting inshore, shelf, shelf-edge, and Gulf Stream waters.

More than 7000 individuals and 25 species, mostly gulls, were encountered on these excursions. Here I document the presence of the unusual species in December, although totals of all birds encountered offshore are in Table 1. Numbers following dates indicate total individuals observed, and locations are given for most sightings. Except for *Catharacta skua* all records discussed are from offshore surveys.

Albatross sp. (*Diomedea*): 22 December 1985 (1, 35°38′N, 74°56′W).—A single immature albatross was seen at a distance as close as 100 m and was studied rather carefully. Nevertheless, its identification remains in doubt. The bird was found over water 200-fathoms in depth. It appeared to be a Yellow-nosed Albatross (*D. chlororhynchos*) but the possibility of an immature Black-browed Albatross (*D. melanophris*) cannot be ruled out. Both species have been reported as rare vagrants in the North Atlantic (McDaniel 1973), and neither exhibits a clear season of occurrence. On the basis of confirmed observations already available (e.g., 3 December 1979 55 mi from Virginia coast) (Am. Birds 34:260, 1980) the chances strongly favor it being a Yellow-nosed Albatross.

Northern Fulmar (*Fulmarus glacialis*): 22 December 1985 (1, 35°32′N, 74°40′W).—Recent population and range expansion of Northern Fulmars in the North Atlantic (Fisher 1952) suggested that this species would become a regular winter resident off the North Carolina coast. Our surveys have shown them present mostly in the fall (October) and early spring (late March) (Lee and Booth 1979 and subsequent pers. obs.). While it could be argued that the growing number of fulmars in the southeast is a result of increased study of the offshore fauna, this is probably not the case. Since the early 1970s there have been at least three birds found on North Carolina's beaches, with no records prior to this time.

Black-capped Petrel (*Pterodroma hasitata*).—Seen on 8 of 11 trips (total number 228), these petrels were found on all December trips to the 500- to 1000-fathom zone. A minimum count of 115 birds was made on 28 December 1982. The birds in December are quite vocal and are less likely to be solitary than in other seasons. "Pairs" are regularly seen in flight following one another. David Wingate (pers. comm.) suggests that the large numbers of December Black-capped Petrels seen off North Carolina may represent prenesting dispersal from breeding islands after burrow sites have been chosen.

Bermuda Petrel (*Pterodroma cahow*): 20 December 1984 (1, 35°32′N, 74°48′W).—The first report of occurrence of a Bermuda Petrel off the southeastern United States was for 18 April 1983 off the Outer Banks (Lee 1984). The problems in separating small *P. hasitata* from *P. cahow* were discussed at that time. The December sighting reported here was over 500-fathoms of water on a day when 36 Black-capped Petrels were seen. Water temperature was 23.9°C. The bird was smaller than any of the Black-capped Petrels, and its dorsal surface was darker than normal for *P. hasitata*. The white rump was greatly reduced and the "collar" was absent. The bird was seen briefly at close range.

Greater Shearwater (*Puffinus gravis*): 12 December 1984 (1, 35°13′N, 74°55′W), 22 December 1985 (2, 35°32′N, 74°46′W; 35°32′N, 74°47′W).—Clapp et al. (1982) provide several reports of Greater Shearwaters for December for the south Atlantic coast: North Carolina, 28 December 1946 (1, Wrightsville Beach), 30 December 1970 (1 Nags Head); South Carolina, 16 December 1964 (2, off Charleston); and Florida, December 1913 (1 found dead N of West Palm Beach); and one for the entire Gulf Coast, 6 December 1977 (1 offshore from Alabama). There are additional winter records for the southeast for other months, and Chris Haney (pers. comm.) saw one off Georgia on 13 December 1984. On 12 December 1984 I collected a single bird 30 miles SE of Oregon Inlet (NCSM 10374), and 2 more were seen in December of 1985. The collected individual had small gonads (5.0 × 17.2), and its weight (593 g) indicated it was in good health. Records of this transequatorial migrant in December in the North Atlantic are unusual, but lingering birds apparently occur with some regularity.

TABLE 1

COUNTS OF SEABIRDS MADE ON 11 OFFSHORE TRIPS OUT OF OREGON INLET, DARE COUNTY, NORTH CAROLINA

	3 Dec. 1982	5 Dec. 1978	5 Dec. 1985	12 Dec. 1984	20 Dec. 1984	22 Dec. 1985	28 Dec. 1982	28 Dec. 1984	29 Dec. 1977	29 Dec. 1984	30 Dec. 1978	Total
Common Loon (*Gavia immer*)			1		2		1			1	1	6
Northern Fulmar (*Fulmarus glacialis*)						1						1
Black-capped Petrel (*Pterodroma hasitata*)	1		6	9	36	1	115	36		24		228
Bermuda Petrel (*P. cahow*)					1							1
Greater Shearwater (*Puffinus gravis*)				1		2						3
Manx Shearwater (*P. puffinus*)	3	1			2	6	1				5	18
Little Shearwater (*P. assimilis*)		1						1				2
Audubon's Shearwater (*P. lherminieri*)	3											3
Wilson's Storm-Petrel (*Oceanites oceanicus*)				153								153
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)		1?	>11									>11
Northern Gannet (*Sula bassanus*)	1	5	(73)[a]	4				(439)	20	5	(375)	976
Red Phalarope (*Phalaropus fulicaria*)	>31	155	8	15	40	1	4		1000's		248	>1502
Pomarine Jaeger (*Stercorarius pomarinus*)	10	1			3							14
Long-tailed Jaeger (*S. longicaudus*)					1							1
Laughing Gull (*Larus atricilla*)	110	1	3	42	41	3		28				228
Bonaparte's Gull (*L. philadelphia*)			2	16	27		1		1000's		62	>1108
Ring-billed Gull (*L. delawarensis*)		1							>10		+[b]	>11
Herring Gull (*L. argentatus*)	80	1	26	451	85	10	33	639	>100	17	+	>1442
Great Black-backed Gull (*L. marinus*)	(>1000)		1	57	2	1	17			5	31	>1116
Black-legged Kittiwake (*Rissa tridactyla*)	16	8	38	9	43	46	33	10	10		28	241
Royal Tern (*Sterna maxima*)								1				1
Forster's Tern (*S. forsteri*)				3				3				6
Bridled Tern (*S. anaethetus*)					2–4							2

[a] Numbers in parentheses are mostly birds seen within 13 km of shore, all others are past the 40-fathom contour.
[b] Indicates species present, but individuals not counted.

Manx Shearwater (*Puffinus puffinus*): 30 December 1978 (5), 3 December 1982 (3), 28 December 1982 (1), 20 December 1984 (2), 22 December 1985 (6).—These sightings suggest that this shearwater is a regular but uncommon species in early winter. The birds are transequatorial migrants, but some may overwinter off the southeastern U.S. coast. Clapp et al. (1982) report single birds (6 December 1978, 8 December 1969, 11 February 1979) from Florida and Texas. Additionally C. Haney (pers. comm.) has records of *P. puffinus* on his trips off Georgia in December and February. A few other beached winter specimens are documented from the Southeast, but since related weather factors and currents that may have transported them are unknown, season of death is not clear. North Carolina specimens collected are all adults of the nominal race *P. p. puffinus* ($N = 14$).

Little Shearwater (*Puffinus assimilis*): 5 December 1978 (1, 35°28′N, 74°52′W), 28 December 1984 (1, 35°16′N, 74°48′W).—Few records of the Little Shearwater are available for the western North Atlantic. The two December records reported here were of individual birds identified primarily by their rapid wing beat and short tails, although the facial markings of one bird were seen well. The birds were not collected but were studied carefully. Water temperature at the 1984 sighting was 23.3°C.

Wilson's Storm-Petrel (*Oceanites oceanicus*): 5 December 1985 (153, 35°37′N, 74°46′W).—Palmer (1962) stated that by November there are no reliable records of this storm-petrel north of the equator and by December; aside from three exceptional records for the vicinity of the Cape Verdes and one from near St. Paul's Rocks, none has been seen north of 30°S. Off the southeastern United States these birds become scarce after mid-September, and the latest record for North Carolina was for 23 October 1979 (pers. obs.). The earliest arrivals were recorded on 2 April 1981. Therefore the occurrence of individuals and flocks of 5 to 40 Wilson's Storm-Petrels was unexpected, and at this time, unexplainable. There were no unusual local weather factors to account for their presence. On the other hand previous winter coverage of the area indicates that occurrence in this season is most irregular. Three birds were collected to confirm identification (NCSM), all were adults and had completed their summer-fall molt.

Leach's Storm-Petrel (*Oceanodroma leucorhoa*): 5 December 1978 (1?, 35°42′N, 75°05′W), 5 December 1985 (>11, 35°37′N, 74°46′W).—Lowery (1974) and Lee (1984) reported the only winter records of Leach's Storm-Petrels for southeastern United States waters. Additionally, one was seen from the Chesapeake Bay Bridge-Tunnel, Virginia, on 10 January 1971 (Am. Birds 25:558–559, 1971). There is a single early-November record for North Carolina (USNM 564835), but, otherwise, middle to late October appears to be the latest the species normally occurs in the western North Atlantic (cf. Clapp et al. 1982). A storm-petrel I believe was this species was seen offshore 5 December 1978. On 5 December 1985 Wayne Irvin and I counted a minimum of 11 Leach's Storm-Petrels along the 500-fathom contour. For the most part they were associated with Wilson's Storm-Petrels. This is the first evidence that the species occurs in U.S. waters, except as an occasional vagrant, after mid-October. To date the earliest known spring migrant for the Southeast is 2 April 1981 (Lee 1984).

Red Phalarope (*Phalaropus fulicaria*): Seen on 9 of the 11 trips (total minimum number 1502).—Although sporadic in occurrence and number, the Red Phalarope is a regular winter resident off the North Carolina coast with numerous records from December through March (pers. obs.). Deep-water feeding concentrations of Red Phalaropes occur along current edges, particularly where large mats of Sargassum have accumulated. When Sargassum is not present these birds are never abundant and often absent entirely. Apparently a large and highly mobile population winters locally off the Southeast coast. The Atlantic winter range was believed to be primarily off the coast of southern South America and western Africa (Clapp et al. 1983), although they are now known to occur with regularity off the southeast United States (Haney 1985, pers. obs.).

Great Skua (*Catharacta skua*): 2 December 1981.—A single female was salvaged from the surf at Cape Hatteras, Dare County, by M. Lyons (NCSM 8171). The bird was a partial albino weighing 593 g. This is the only specimen record for the state, and the second documented occurrence for this species in North Carolina. Lee and Rowlett (1979) reported a band recovery from Cape Lookout, Carteret County, N.C., on 29 December 1975. This bird had been banded five months previously in Iceland. These two records constitute the only documentation of *C. skua* on the southern United States coast.

Long-tailed Jaeger (*Stercorarius longicaudus*): 20 December 1984 (1, 35°15′N, 74°40′W).—Although precise limits of wintering areas are unknown, Harrison (1983) indicates the species winters in the southern hemisphere off South America and the west African coast from November to March. The sixth addition of the AOU Checklist (1983) states that these birds winter from latitude 40°N southward, but Cramp et al. (1983) states that wintering areas are "evidently all in southern hemisphere since only exceptionally found north of equator December–March . . . ." The winter status of Long-tailed Jaegers in the northern hemisphere is in need of review.

The North Carolina record appears to be quite unusual in that North American winter records are very scarce, and problems of identifying jaegers in nonbreeding plumage make existing records difficult to assess. Winter sight records include two for South Carolina, 21 December (1896) and 3 February (1908), and several for Florida, the most recent being 30 January 1983 off Cape Canaveral (Am. Birds 37:295, 1983). The only verified evidence of winter occurrence in the Southeast, however, is a single 1889 specimen record for the Gulf Coast of Florida. It was originally identified and reported as *S. parasiticus* by Scott (1889). The December bird seen off North Carolina was subadult with elongated, but not fully grown, central tail feathers.

Bridled Tern (*Sterna fuscata*): 20 December 1984 (2–4, 35°13′N, 74°49′W).—This is the only record for North Carolina between 12 October and 17 April (date limits from Lee and Booth 1979 and subsequent pers. obs.). Although there are no winter records of these terns to the north, additional records for this period to the south are available for the Atlantic coast of Georgia (Oriole 49:19, 1984; 50:19, 1985) and Florida (Clapp et al. 1982). Water temperature at the site of the 20 December sighting was 17.8°C.

Discussion.—The birds reported above come from a wide array of geographic origins. Three species, Bermuda Petrel, Black-capped Petrel, and Bridled Tern are tropical and subtropical species occurring in the western Atlantic. Records now indicate that Black-capped Petrels are regular inhabitants of deep waters off the southeastern United States at all seasons. The same may be true for Bermuda Petrels, but their small population and identification problems at sea limit opportunity for verified encounters. Bridled Terns, though common in the warmer months, are not known or expected to occur regularly in the Southeast in the winter. The Little Shearwater is a transoceanic visitor.

The remaining nine birds are largely long-distance migrants, with most believed or assumed to be obligate transequatorial migrants. Two species, Greater Shearwater and Wilson's Storm-Petrel, are of southern hemisphere origin, spending the austral winter in the northern hemisphere. A third, the unidentified albatross, is also from the southern hemisphere. Northern Fulmars, Manx Shearwaters, Leach's Storm-Petrels, and Great Skuas are of boreal North Atlantic origin; Red Phalaropes and Long-tailed Jaegers nest in the Arctic tundra. Four of these birds winter chiefly in the southern hemisphere. Great Skuas are believed to be essentially confined to the North Atlantic, but confirmed records for the southeastern United States are limited to the two birds discussed above. Northern Fulmars are confined to the northern hemisphere. In that most of the more unusual species discussed here are represented in this study by only a few individuals and common species numbers fluctuate

erratically, it appears that the deep water zone off North Carolina's Outer Banks is not a major wintering area for marine birds.

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First record of the Grey-chinned Hermit (*Phaethornis griseogularis*) west of the Colombian Andes, with notes on the displays of the species.—The range of the Grey-chinned Hermit (*Phaethornis griseogularis*) covers western Venezuela, northwestern Brazil, eastern Colombia (Deptos. de Meta, Caquetá, Putumayo), eastern Ecuador and Peru (Meyer de Schauensee 1964). The westernmost record of the species from El Cauca in northwestern Colombia (08°10′N, 73°24′W) is questioned by Meyer de Schauensee (1949). Olivares (1969) reported a more widespread distribution for this hermit in Colombia, but this is not supported by sight records.

Distribution.—In July and August 1976 and January and February 1977, I carried out extensive field work on the altitudinal distribution of hummingbirds in the western Andes near Cali (Depto. del Valle), in southwestern Colombia. In both years, the mountains around Lago Calima (03°55′N, 76°30′W), a fresh-water reservoir, were the westernmost localities where data were collected. Time was spent mainly in the transitional zone between tropical and subtropical forests along the mountain ridge "Vereda el Remolino" (altitude 1350 m). Here, hermits (Phaethornithinae) were represented by White-tipped Sicklebills (*Eutoxeres aquila heterura*), Tawny-bellied Hermits (*Phaethornis syrmatophorus syrmatophorus*), and Grey-chinned Hermits. The rufous-orange belly clearly distinguishes the latter species from the closely related trans-Andean subspecies of the Little Hermit (*Phaethornis longuemareus subrufescens*), which has ochre-yellow underparts. *P. l. subrufescens* was also present in the valleys around Lago Calima below 600 m, and was restricted to semiarid vegetation. To my knowledge, the Grey-chinned Hermit has never been reported in central and western Colombia, and this record does not fit into the presently known zoogeographic cis-Andean pattern of the species. It is hard to believe, however, that birds found in the mountain range around Lago Calima represent an isolated population, as the external morphology and biometrical data agree perfectly with those obtained for the eastern Andean population (N = 17 males, 41 females). The only explanations I have at hand are that either the species was overlooked in the field or has been mistaken for the subspecies of the Little Hermit. This opinion is supported by a communication from C. Hinkelmann, presently in Bogotá, stating that 2 males of the Grey-chinned Hermit, misidentified as Little Hermits, are in the scientific collection of the Universidad Nacional de Colombia, Bogotá, both originating from the Depto. de Nariño, southwestern Colombia, namely from Juanambu (01°35′N, 77°25′W) (collection No. 7951), and from Valle del Patia (02°13′N, 78°40′W) (collection No. 7956). Three specimens (ZFMK Nos. 86.001, 86.002, 86.003) of *Phaethornis griseogularis* from "Vereda el Remolino," Lago Calima, are deposited in our collection.

Behavior.—In January 1977, I discovered a lek of 6 male Grey-chinned Hermits at an altitude of 1200 m. The display ground, covering an area of approximately 60 m^2, was along an exposed southwestern slope of sparse secondary vegetation shaded by primary forest. Males attended the assembly during most of the day, with peak singing activity in the early morning (08:00–10:00) and in the afternoon (15:00–16:00). Males sang from horizontal perches 40–60 cm above the ground. When displaying, each male uttered a high-pitched rapid "warbling" song (*tzee, weeh-weeh-tzee-dee*), first ascending in pitch, and then descending. While vocalizing, the males held their bills upright and slightly open, exposing their black and yellow lower mandible, and wagged their tails constantly.

An individual singer's territory within the lek comprised an area of approximately 10 m^2 and included 3–5 traditional perches. It was surrounded by low (approximately 1 m) scattered shrubs, and males could hear but not see their neighbors.

As display territories within the lek had a patchy distribution, I decided to study the courtship behavior of 2 males (males A and B). Both birds were observed from a blind, 3

FIG. 1. (A) Frontal aerial display of *Phaethornis griseogularis,* (B) rapid flight display, (C) pre-copulatory approach.

m away from the main singing spot for a total of 8 h during 2 days (3 h in the early morning, 5 h in the afternoon). During the time of observation, a total of 13 visits by intruders was recorded for both display grounds. In 9 cases intruding individuals were spontaneously driven out of the courtship territory by the owner. Sexes are alike, and I assumed that intruders were males. Aggressive encounters between males A and B were not observed. Conspecifics allowed to land on the song perch of the owner presumably were females, as courtship display was immediately performed. Male A received a total of 9 visits, 3 of which led to copulation; male B had 4 visits, one of which led to mutual displaying, but not to copulation. In the morning the mean presence of male A on the lek was 21 ± 8 min [SE] while his mean absence was 15 ± 9 min. The corresponding data of male B are 20 ± 5 min and 18 ± 8 min, respectively. Similar data were not recorded during the afternoon.

Males displayed when a female landed on the singer's perch. Normally, the stationary male directed his song towards the arriving bird, keeping his bill upright and exposing his black and yellow mandible. Thereafter, 3 phases of aerial display occurred (Fig. 1). Males took to the wing, wafting in front of the female, and executed a horizontal arc (Fig. 1A). Once airborne, they fanned their tails upright while holding their feet in front of their bodies. Their wings beat against the upright rectrices, producing a mechanical sound that amplified the humming of the wing beats. During this stage of frontal courtship, males sang (subdued warblings), sometimes protruding their tongues. This display lasted up to 2 min, but was often less than 1 min. Males then flew rapidly back and forth about 10 cm above the perched female (Fig. 1B), producing sharp snapping sounds and spreading apart the rami of their lower mandibles, to almost twice that of the closed bill (not shown in Fig. 1). During this maneuver, the male's bill was only slightly open and pointed down towards the female, who watched his flight. The yellowish mouth lining seen when opening the species' bill by hand was not exhibited during the display. Males repeated their maneuvers 4–6 times, whereupon they reduced their flight speed and hovered above the female's back (Fig. 1C). The female

then lowered her wings and exposed her back, indicating her readiness for mating, and the male landed dorsally on the perched female.

Published records on the courtship display of members of the genus *Phaethornis* are available only for *Phaethornis superciliosus, P. guy, P. longuemareus,* and *P. ruber* (Davis 1934, 1958; Skutch 1951; Arp 1957; Snow 1968, 1973, 1974; Mobbs 1971; Stiles and Wolf 1979). Here, I restrict discussion to a comparison of mutual display of *griseogularis* with the species most closely allied to it, namely *P. longuemareus* and *P. ruber.* Perching display: Stretching and yawning-like movements observed by Snow (1973) and Davis (1934) in *P. ruber* and *P. longuemareus* were not witnessed in *P. griseogularis.* Aerial display: In all 3 species the male, tail erected, hovers in front of the stationary female. *P. ruber* and *P. griseogularis* sing towards the potential mate, whereas singing in *P. longuemareus* was not observed. In the latter, more elaborate stages of aerial displays were noted (e.g., backward and up-and-down rotations) (Skutch 1951, Arp 1957). In the subsequent phase, rapid flicks or quick flight movements with gape display are exhibited by all 3 species; variations of certain postures (e.g., tongue protrusion) were observed in *P. ruber* (Davis 1958, Mobbs 1971). Similar flight patterns are known in larger hermits, (e.g., *P. superciliosus, P. guy*) (Snow 1974, Stiles and Wolf 1979), suggesting relatively stable interspecific courtship components. Thus, the male courtship display of *P. griseogularis* is intermediate in form between *P. ruber* and *P. longuemareus,* linking the behavior of the 3 species.

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Estimating relative abundance of forest birds: simple versus adjusted counts.—In applied studies of avian ecology, one of the more commonly encountered problems is the estimation of a species' abundance across a gradient of habitat types. Recently, much attention has focused on transect or point counts incorporating detection functions derived from the distribution of distances to each detected bird (Verner 1985). Detection functions are used to calculate a "basal region" (Emlen 1971), which is that area sampled over which all individuals are believed to be detected. The count is adjusted by dividing by the basal region for any particular habitat, and this adjusted count is an estimate of the species' density in that habitat. Assuming equal sampling effort, variation of density estimates among these habitats is thus a function of two variables: (1) variation in the number of birds counted in each habitat, and (2) variation in size of basal region. If, for any particular species, basal region does not vary in size among habitats, then any variation in estimated density among these habitats can be attributed to variation in the number of birds counted. In this case, simple counts might provide as good an estimate of relative abundance across habitats as the more sophisticated adjusted counts. The purpose of this paper is to investigate how well simple counts compare to more complex methods of estimating relative abundance.

Study area and methods.—As part of a larger study on habitat associations of forest vertebrates (Raphael 1984), I established 136 study plots in forests dominated by Douglas-fir (*Pseudotsuga menziesii*) in association with tanoak (*Lithocarpus densiflora*), Pacific madrone (*Arbutus menziesii*), canyon live oak (*Quercus chrysolepis*), and black oak (*Q. kelloggii*). All plots were in the Trinity and Klamath river drainages of northwestern California, at elevations between 427 and 1220 m. Plots were defined by the boundaries of timber stands delineated on U.S. Forest Service timber-type maps.

To characterize the structure and composition of vegetation on each plot, I randomly selected three 0.04-ha circular subplots within a 90-m radius of the plot center (a total of 408 subplots). Within each subplot, I recorded species, height, diameter, and crown dimensions of each shrub or tree >2 m tall. These measurements yielded an estimate of the canopy volume of each tree; volumes of trees were summed to estimate total canopy volume on each plot (Table 1) using a modified version of the program HTVOL (Mawson et al. 1976).

An index of stand age was calculated for each plot using a basal-area-weighted average of the ages of all conifers on the 3 subplots (Raphael 1984). I estimated the age of a tree from its diameter using a regression analysis of an extensive sample of known-aged trees previously measured within the study area (Table 1). I also calculated an index of the yearly solar radiation (Frank and Lee 1966) to which each site was exposed. This index was based on slope, aspect, and latitude. Values were largest on south-facing, moderate slopes and smallest on north-facing slopes (Table 1).

Birds were counted from a point marked with plastic flagging at the approximate center of each of the 136 plots. All points were at least 360 m apart. Each plot was visited shortly after sunrise on 4 days each year during May and June 1981–1983. On each visit, an observer recorded the estimated distance to each bird seen or (more often) heard during three successive 10-min periods (for a total of 36 10-min counts per plot). Special care was taken to record a bird only once during each period, and to record observations independently among the three successive periods.

The data were analyzed in three ways. First, I simply counted the total number of detections of each bird species recorded during the 36 10-min counts at each plot over all three years. Birds detected at distances >180 m (one-half of the minimum distance between adjacent plot centers) were excluded.

TABLE 1

CHARACTERISTICS OF DOUGLAS-FIR STANDS IN RELATION TO STAND AGE CLASS IN NORTHWESTERN CALIFORNIA

Characteristic	Stand age class (year) 50–150		150–200		200–250		250–300		>300		Significance
Average age	124	(55–146)[a]	178	(155–199)	229	(203–248)	272	(254–300)	329	(302–369)	N.T.[b]
Coniferous canopy volume[c]	56.1	(0.7–91.7)	52.5	(3.9–141.5)	50.4	(10.5–133.0)	42.3	(5.9–106.2)	43.3	(5.4–85.3)	>0.05
Hardwood canopy volume[c]	15.6	(0.5–34.3)	16.2	(0.0–41.8)	29.2	(1.0–91.2)	28.9	(5.2–49.0)	33.4	(12.4–83.9)	<0.001
Density (N/ha) of stems <53 cm dbh	1050	(400–2650)	964	(250–1842)	1097	(425–2600)	1416	(292–2833)	1517	(417–3075)	<0.001
Density (N/ha) of stems ≥53 cm dbh	47	(0–83)	63	(8–183)	60	(17–117)	56	(8–142)	52	(17–108)	<0.001
Elevation (m)	660	(366–1129)	819	(475–1220)	843	(442–1159)	882	(549–1280)	937	(610–1159)	<0.001
Solar radiation index[d]	0.49	(0.25–0.60)	0.51	(0.38–0.59)	0.47	(0.25–0.6)	0.47	(0.24–0.60)	0.38	(0.24–0.59)	<0.001
Number of sites	27		25		31		32		21		N.T.

[a] Mean (range).
[b] N.T. = not tested.
[c] Expressed as thousands of m^3/ha.
[d] Index of potential yearly solar radiation. Larger values indicate warmer, drier sites.

TABLE 2

SPEARMAN RANK CORRELATION BETWEEN THREE ESTIMATES OF RELATIVE ABUNDANCE OF BREEDING BIRDS AND THREE ENVIRONMENTAL GRADIENTS IN DOUGLAS-FIR FORESTS OF NORTHWESTERN CALIFORNIA, 1981–83

Bird species and environmental gradient	Correlation of gradient with:		
	Total count	Fourier density	Emlen density
Black-headed Grosbeak			
Stand age	−0.04	−0.02	0.00
Solar radiation	0.06	0.06	0.04
Elevation	−0.36[c]	−0.39[c]	−0.37[c]
N[d]	136	130	128
Hermit Warbler			
Stand age	0.23[b]	0.18[a]	0.20[a]
Solar radiation	−0.28[c]	−0.31[c]	−0.35[c]
Elevation	0.48[c]	0.43[c]	0.42[c]
N	136	132	128
Western Flycatcher			
Stand age	0.18[a]	0.16	0.10
Solar radiation	−0.13	−0.11	−0.15
Elevation	−0.24[b]	−0.25[b]	−0.25[b]
N	136	136	128
Western Tanager			
Stand age	−0.43[c]	−0.35[c]	−0.34[c]
Solar radiation	0.18[a]	0.22[a]	0.16
Elevation	−0.40[c]	−0.35[c]	−0.35[c]
N	136	122	128

[a] $P < 0.05$.
[b] $P < 0.01$.
[c] $P < 0.001$.
[d] Number of sites sampled for which an abundance estimate could be calculated.

Second, I used the distance estimate to each of these birds to calculate a density estimate for each species with sufficient sample size (N > 30) at each plot, using the computer program TRANSECT (Laake et al. 1979). Because this program is designed to analyze transect data, several modifications were necessary to apply it to point data. All distances were transformed to area by treating each distance estimate as a radius. That is, I squared each distance and multiplied by π, and these new values were substituted for the original raw distances. The number of censuses (36) per plot was equivalent to transect line length in the program. The value actually entered into the program was one-half of the number of censuses (18) to adjust for the constant (2) in the computer algorithm that doubles line width. All data were truncated to an equivalent distance of 180 m (10.2 ha after transformation). Density estimates were calculated using the Fourier series estimator (Burnham et al. 1981).

The third analysis was a calculation of density modified from Emlen's original (1971) method. For this analysis, distances were grouped by 5-m intervals out to 20 m, and thereafter into 10-m intervals. The cumulative number of birds detected out to each interval was then calculated, and a density was estimated for each additional interval by dividing the count

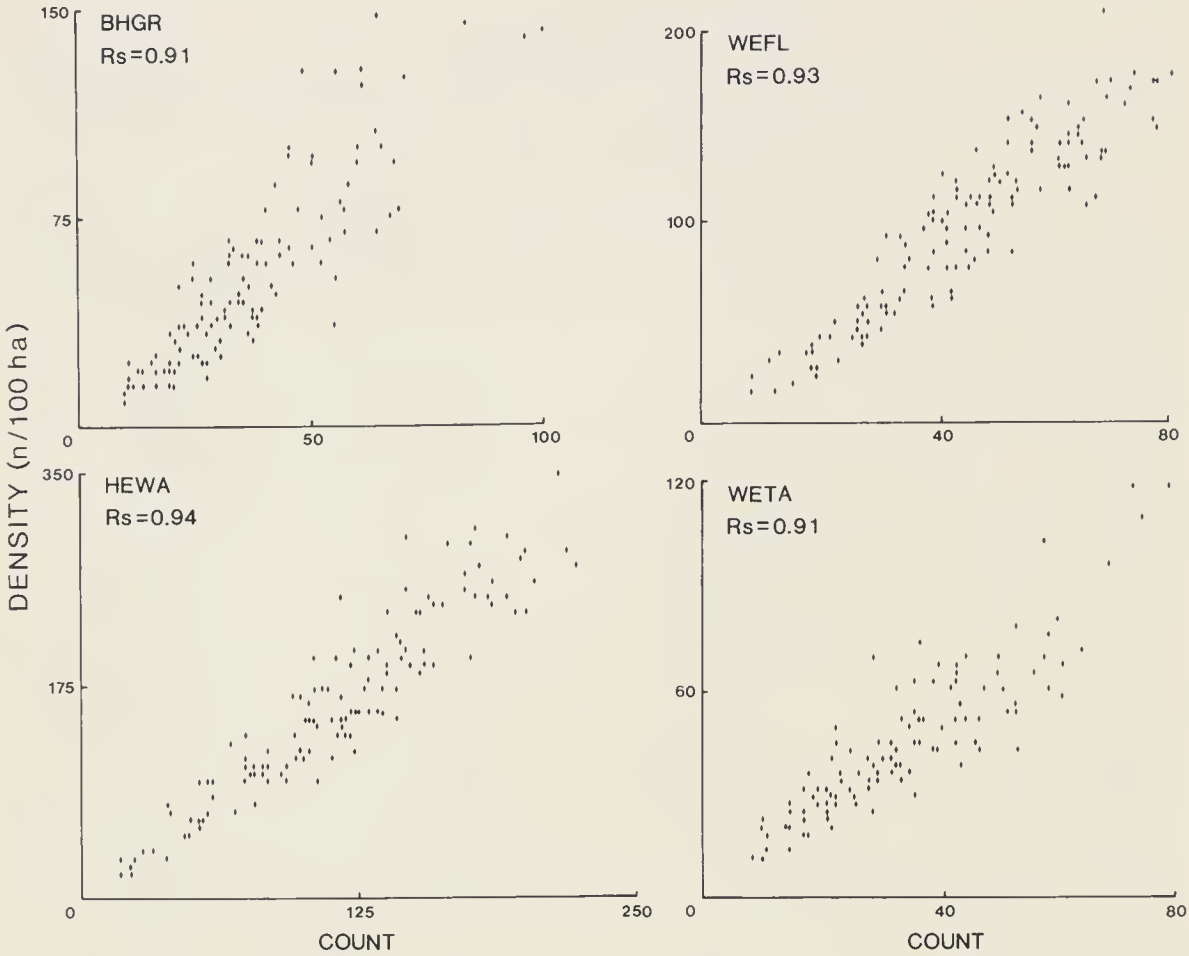

FIG. 1. Relationship of simple counts to density estimates calculated using the Fourier series estimator of program TRANSECT for four breeding bird species in Douglas-fir forests of northwestern California, 1981–83. BHGR = Black-headed Grosbeak, HEWA = Hermit Warbler, WEFL = Western Flycatcher, WETA = Western Tanager. Spearman rank correlation coefficients are listed below each bird-species code.

by the area represented by each interval. The maximum density calculated from this series of successively larger intervals was taken as the best estimate.

To evaluate how the two density estimates and the total count ranked the abundance of species across habitats (within Douglas-fir forests), I computed the Spearman rank correlation between the abundance estimates and each of three major environmental gradients (stand age, solar radiation index, elevation). I also compared the mean number of birds counted and the mean density for the two estimators among 5 stand age-classes using one-way analysis of variance.

To calculate the contributions of variation in numbers counted and basal region on variation in density among habitats, I computed the squared coefficient of variation (CV^2) for the count and for the basal region for each species among all plots for which a density estimate was derived. Burnham et al. (1980:51) showed the CV^2 of a density estimate is equal to the sum of the CV^2 for the count and effective area. Therefore, the percentage of the CV^2 of density attributed to the count or basal region was easily calculated and was used to assess the relative contribution of each source of variation.

Results.—Four species were sufficiently abundant to calculate population density estimates

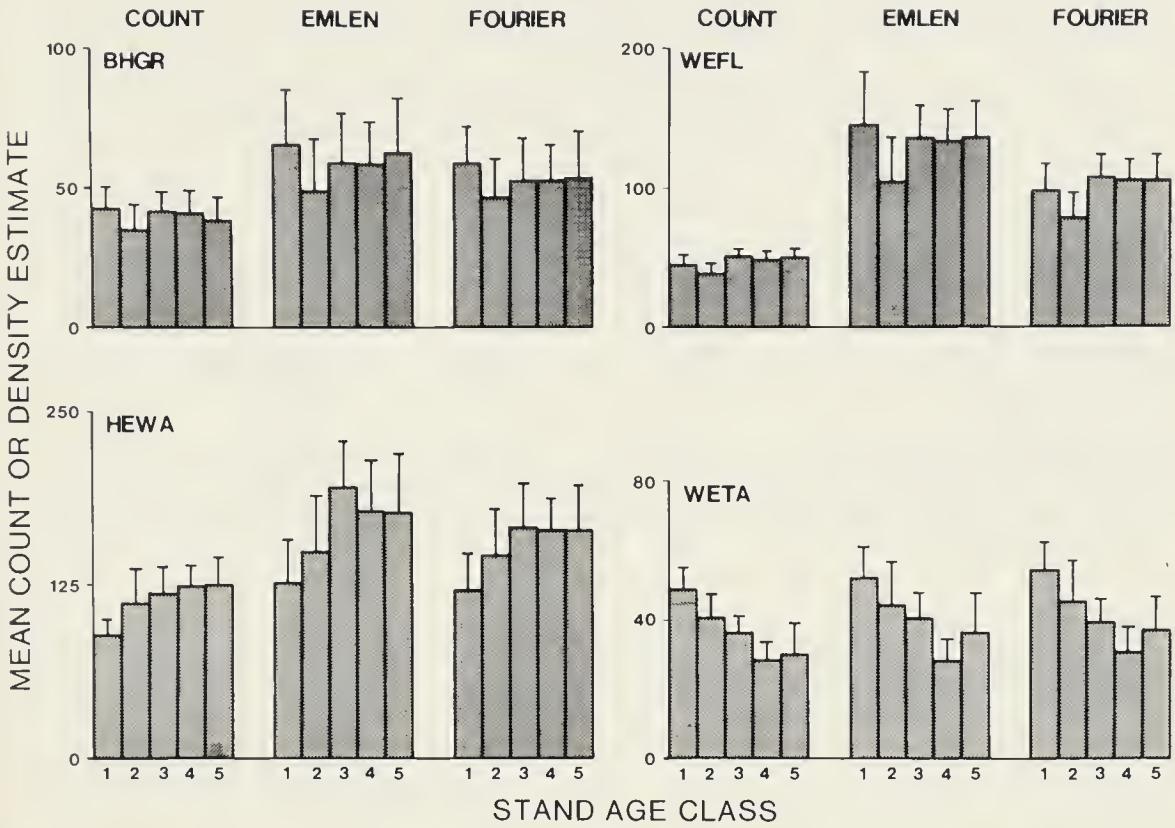

FIG. 2. Comparison of mean abundance derived from counts, and 2 density estimators for 4 species of breeding birds among 5 stand age classes of Douglas-fir forests of northwestern California, 1981–83. Vertical lines indicate 95% confidence intervals. Stand age classes are described in Table 1. See Fig. 1 for species abbreviations.

for nearly all sites: Hermit Warbler (*Dendroica occidentalis*) (N = 15,352), Western Flycatcher (*Empidonax difficilis*) (N = 6265), Black-headed Grosbeak (*Pheucticus melanocephalus*) (N = 5445), and Western Tanager (*Piranga ludoviciana*) (N = 5036). The three estimators yielded similar correlations with each of the three environmental gradients for each bird species (Table 2). All estimators suggested, for example, that the Hermit Warbler was most abundant in older, cooler, high elevation sites, whereas the Western Tanager was more abundant in younger, warmer, low elevation sites. The similarity of these habitat correlations resulted from the strong correlations among the estimators themselves, illustrated for the simple counts vs Fourier estimator (Fig. 1).

The similarity of results using the three estimators also is apparent from comparisons of mean abundance among the 5 stand-age classes (Fig. 2). Whereas the absolute magnitude of the abundance estimates varied, the relative magnitudes among the age classes were quite similar. For nearly all comparisons, the rank order of abundance among age classes was consistent among estimators. The one exception was that, for Hermit Warbler, the mean count was highest in age class 5 (>300 yr). None of the differences, however, was statistically significant, considering the breadth of the confidence interval about each mean (Fig. 2).

The analysis of the sources of variance in the density estimates of these 4 species showed that variation in count contributed from 73 to 84% (Table 3). For any of these species, then, variation in basal region among plots was only a minor component of variation in density.

Discussion.—My results show that for the habitats I studied variation in the density estimates of bird species along habitat gradients is much more strongly influenced by vari-

TABLE 3

SQUARED COEFFICIENTS OF VARIATION OF THE SIMPLE COUNT, BASAL REGION[a], AND DENSITY ESTIMATE AMONG DOUGLAS-FIR FOREST SITES, NORTHWESTERN CALIFORNIA, 1981–83

Bird species	Squared coefficient of variation			Percent contribution of count
	Simple count (C)	Basal region (BA)	Density estimate ($C + BA$)	$C/(C + BA)$
Western Flycatcher	0.150	0.036	0.186	80.6
Western Tanager	0.194	0.060	0.254	76.4
Hermit Warbler	0.205	0.041	0.246	83.5
Black-headed Grosbeak	0.260	0.095	0.355	73.3

[a] Basal region is approximately the inverse of $f(0)$, calculated using the Fourier series estimator in program TRANSECT (Burnham et al. 1980).

ation in the simple count than by variation in basal region. This result is shown explicitly in Table 3, and is implicit in Table 2 and Figs. 1 and 2. That the count is correlated with density (Fig. 1) is certainly expected because the count is itself the numerator in the calculation of density. Also important, however, are the strength of the correlation and the fact that little additional information is contained in the basal region component. The surprising result is that an unadjusted count was apparently as good an index of abundance as either of the more sophisticated density estimates I evaluated.

These results do not imply that investigators should abandon density estimation in favor of simple counts. Clearly this is undesirable on a number of grounds, particularly because simple counts cannot account for between-species differences in basal region size, which are probably much stronger than the within-species, between-habitat differences I report here. Rather, these results suggest that investigations on the sources of count-variation should receive greater emphasis. Many studies (see papers in Ralph and Scott 1981) have addressed the need to adjust for basal regions of birds in different seasons, times-of-day, habitats, etc., but few have discussed variation in numbers of detections. Results of this study, although limited to only a few species in one forest type, suggest the need to focus more clearly on this important component of density. In addition, this study provides evidence that if relative abundance is what one wants to estimate, simple counts can be as good an estimator as more complex estimators adjusted by basal region.

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A synthetic diet for fruit-eating birds.—Long-term maintenance of fruit-eating birds has been a major barrier to their study in captivity. Recently captured birds lose weight rapidly, even when feeding on fruits ad libitum. Birds under 50 g may lose weight so rapidly that flight muscles are seriously weakened; death may occur within a few days of capture (Moermond, Denslow, and Levey, pers. obs.). Studies using recently captured birds in poor physiological condition are unlikely to yield consistent or interpretable results. It is therefore important that experimental animals be maintained at good nutritional and energetic levels before behavioral experiments are initiated.

In this paper we describe a synthetic diet for maintaining captive fruit-eating birds, with notes on its use. We have been able to keep 25 species of tropical and temperate fruit-eating birds on this diet at steady weight and in good plumage for periods of up to 12 months. Some of these birds were recaptured in good condition months after their release.

We have used captive fruit-eating birds maintained on this diet for a variety of behavioral studies (Moermond and Denslow 1983, 1985; Levey et al. 1984). The diet is not only useful for maintaining experimental birds but can be manipulated as an experimental tool.

The diet.—The synthetic diet consists primarily of a mixture of mashed ripe bananas, soy protein isolate, and a supplement of vitamins and minerals in an agar-based gel (Appendix 1).

A protein gelatin (i.e., Knox®) may be an acceptable substitute for agar where the latter is either too expensive or unavailable. An agar or gelatin base makes the diet easy to handle, insures a uniform composition of the mixture, and precludes selection of only the more palatable components of the mixture by the birds. At warm temperatures (>25°C) under which our birds were held, the food ferments quickly; we replaced it twice daily, at sunrise and at noon. A mold retardant such as ascorbic acid could be added to retard rapid deterioration, although we have not done so.

Habituation techniques.—The yellow-brown mash bears little resemblance to brightly-colored fruits frugivores normally eat, and is thus often not recognized as food by naive birds. Newly caught birds therefore must be habituated to the mixture after capture.

TABLE 1

NUTRIENT AND CALORIC CONTENT OF SYNTHETIC DIET FOR FRUIT-EATING BIRDS (VALUES ARE CALCULATED FROM PUBLISHED DATA ON THE COMPOSITION OF THE DIET CONSTITUENTS [WATT AND MURIEL 1963] AND DATA SUPPLIED WITH THE SOYBEAN PROTEIN ISOLATE [U.S. BIOCHEMICAL CORPORATION, CLEVELAND, OHIO 44128])

	g/100 g dry weight
Protein	16.3
Fat	5.0
Carbohydrates	73.6
Fiber	5.0
Calcium	0.18
Phosphorus	0.34
Iron	0.25
Sodium	0.20
Potassium	0.72
Water	86%
Energy content (Kcal)	425.7

We have had the most success inducing naive birds to eat the diet after it was cut into small cubes (3 × 3 × 3 mm) and colored with red or blue food coloring. Natural berry juices (e.g., Pokeberry [*Phytolacca* spp.]) can also be used to stain the gel. The cubes, thus simulating berries, should be presented with a few natural berries in a small dish near a perch. Most birds will eat the berries and then sample the colored cubes. More berries should be added if no cubes are eaten within 1–2 h. Once the bird has begun to eat colored cubes, these can be presented on top of similarly colored food that has been mashed or broken up with a fork. The number of cubes should be decreased gradually and embedded in the colored mash until the bird eats the mash. The amount of color added to the mash can then be reduced to several spots and, finally, eliminated. The entire process usually takes 4–7 days. All individuals we tested learned more quickly when caged with a conspecific already feeding on the diet. Captive Cedar Waxwings (*Bombycilla cedrorum*), Gray Catbirds (*Dumetella carolinensis*), and Swainson's Thrushes (*Catharus ustulatus*) ingested about twice their body weights in fresh food daily, although the exact amount varied among species and depended on such factors as protein content and ripeness of the bananas (Denslow and DeVito, unpubl. data).

Birds that take most of their fruits on the wing (e.g., Pipridae, Trogonidae, Tyrannidae) are the most difficult to habituate. These birds pluck and swallow whole fruits presented away from foliage (Moermond and Denslow 1985). We have always found it necessary to use brightly colored cubes of the gel when training such birds. Murphy and King (1982) also found that captive Cedar Waxwings, another sallying species, more readily ate an artificial diet if presented in berry-like lumps. In contrast, tanagers are relatively easy to train, readily accepting the diet. We have been able to start them on the diet simply by placing fruits on top of and mixed with mashed colored gel.

Nutritional, caloric, and water contents of the diet (Table 1) fall within the ranges of those reported from natural fruits (Stiles 1980, Wheelwright et al. 1984). In comparison with fruits from the 29 tropical plant families surveyed by Moermond and Denslow (1985), the banana

TABLE 2

SPECIES OF FRUIT-EATING BIRDS MAINTAINED SUCCESSFULLY ON THE ARTIFICIAL DIET, AND THE EASE WITH WHICH THEY WERE KEPT

Species	Ease of maintenance[a]
Slaty-tailed Trogon (*Trogon massena*)	++
Collared Araçari (*Pteroglossus torquatus*)	+++
Ochre-bellied Flycatcher (*Mionectes oleagineus*)	+
Gray-capped Flycatcher (*Myiozetetes granadensis*)	+
White-ruffed Manakin (*Corapipo altera*)	++++
White-collared Manakin (*Manacus candei*)	++++
Red-capped Manakin (*Pipra mentalis*)	++++
Swainson's Thrush (*Catharus ustulatus*)	+++
Wood Thrush (*Hylocichla mustelina*)	+++
Pale-vented Thrush (*Turdus obsoletus*)	+++
Gray Catbird (*Dumetella carolinensis*)	+++
Cedar Waxwing (*Bombycilla cedrorum*)	++++
Scrub Euphonia (*Euphonia affinis*)	++++
Olive-backed Euphonia (*E. gouldi*)	++++
Red-throated Ant-Tanager (*Habia fuscicauda*)	+++
Dusky-faced Tanager (*Mitrospingus cassinii*)	+
Scarlet-rumped Tanager (*Ramphocelus passerinii*)	++++
Tawny-crested Tanager (*Tachyphonus delatrii*)	+
Plain-colored Tanager (*Tangara inornata*)	+++
Golden-masked Tanager (*T. larvata*)	+++
Blue-gray Tanager (*Thraupis episcopus*)	+++
Palm Tanager (*T. palmarum*)	++++
Black-faced Grosbeak (*Caryothraustes poliogaster*)	+
Buff-throated Saltator (*Saltator maximus*)	++
Orange-billed Sparrow (*Arremon aurantiirostris*)	+

[a] + = Accepted diet after 7 days, but weight fluctuated widely. We found it necessary to supplement the diet with insects. Adjusted well to captivity and behavioral experiments. ++ = Accepted diet (usually in 7 days) and maintained capture weight, but did not adjust well to captivity or behavioral experiments. +++ = Accepted diet in 7 days, maintained capture weight, and adjusted well to captivity and behavioral experiments. ++++ = Accepted diet within 3 days, maintained weight, and adjusted well to captivity and behavioral experiments.

diet is rich in proteins and carbohydrates and low in lipids. The median protein content was 8.4% (dry weight) for 29 families of tropical fruits in the survey compared to approximately 16.3% in the synthetic diet. Although it is likely that fruit-eating birds depend on fruits primarily as an energy source and supplement the fruit component of their diets with insects (Moermond and Denslow 1985), species vary widely in their dependence on nonfruit protein sources. The diet is therefore not equally suitable for maintaining all species of fruit-eating birds (Table 2). We have had difficulty maintaining some frugivorous finches (e.g., emberizids such as *Caryothraustes poliogaster, Cyanocompsa cyanoides*), some species of tanagers (e.g., *Tachyphonus* spp. and *Mitrospingus cassinii*), and frugivorous flycatchers (e.g., *Myiozetetes* spp. and *Mionectes* spp.). Although all these species commonly feed on fruit in the field (Jenkins 1969, Fitzpatrick 1980), they were maintained successfully in cages only by supplementing the synthetic diet with live insects. Alternatively, the protein content of

the diet could be increased slightly (although increased addition of the soy isolate makes the texture unacceptable for some birds).

Maintenance of captive birds.—We suggest that each bird's weight be followed closely, at least until weight has stabilized and the bird is fully habituated to the diet. Remote weighing devices eliminate trauma to the bird while it is being weighed. After an initial slight loss of weight, birds usually regained capture weight within 2 weeks. Weights of captive birds kept on this diet have generally fluctuated within 5% of capture weight.

Two sources of water should be provided: a tube for drinking and a dish for bathing (the latter is critical for maintenance of healthy plumage). Birds can often be induced to bathe if sprayed with a fine mist of water and learn quickly if in a position to observe other birds bathing.

If the birds are to be kept outside, care should be taken to provide adequate shade and protection from wind, rain, and predators. In Costa Rica, ants (*Solenopsis* sp.), bees (*Trigona* sp.), rats (*Rattus* sp.), and snakes (Boa constrictor, *Pseustes poecilonotus*) were constant problems. Ants and bees feed on the gel, preventing the birds from feeding. Ants can be controlled with Tanglefoot® on all points of access to the cages. Sturdy, tightly sealed cages are the best protection against bees and predators.

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Appendix 1

Ingredients for approximately 2 l of food:

1 l water
11 g agar (approximately)
1.5 g sodium chloride
1.6 g dicalcium phosphate
1.5 g complete vitamin and mineral supplement for birds[1]
25 g soy protein isolate
7 g vegetable oil
37 g wheat germ
680 g mashed bananas, fully ripe

Directions:

Carefully stir agar into rapidly boiling water, preferably with a whisk, continuing to stir until water comes again to a rolling boil and the agar is completely dissolved. If the agar does not dissolve, the food will not "set" firmly. In a separate dish, mix the soy isolate with a small amount of water to make a paste. Thoroughly stir the paste and remaining ingredients into the mashed bananas. Add the agar solution and mix well. Check the sugar concentration with a refractometer and, if necessary, bring the mixture up to approximately 10% with glucose. Place in covered containers and refrigerate. The appropriate amount of agar varies depending upon the brand and purity. The mixture should congeal at room temperature, but also should be easily mashed with a fork. It will keep for approximately one week under refrigeration, but may also be frozen. The texture of thawed gel is much less cohesive but still adequate as a maintenance diet. Only fully ripe bananas should be used because all birds prefer them over slightly unripe bananas, which are poorly assimilated.

[1] We have used 8in1® Vitamin Mineral Supplement for Birds, made by 8in1 Pet Products, Inc., Brentwood, New York 11717.

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Bathing behavior of nesting Prairie Falcons (*Falco mexicanus*) in southwestern Idaho.—During 1984 and 1985 we observed 24 Prairie Falcon pairs nesting in the Snake River Birds of Prey Area (BOPA), in southwestern Idaho, from egg laying and incubation through brood rearing until the chicks were 35 days of age (a total of about 4400 h of observation). During this period we recorded 34 dustbaths: 4 were taken by males (3 different individuals) and 30 by females (8 different individuals). All dustbaths were taken on sections of cliffs where a layer of sandstone was exposed and a ledge was available. The falcons landed on these ledges and shuffled on their abdomens through the fine sand with the body feathers fluffed out and their wing and tail feathers partly extended. Dustbathing birds frequently made dipping motions with their heads and bodies. Dustbathing was followed by extensive preening of breast, wing, and tail feathers, and, finally, by shaking of the entire body. Dustbathing averaged 4.7 ± 5.7 min [SD] (range = 1–13 min, N = 4) for males and 2.1 ± 1.6 min (range = 1–6 min, N = 30) for females. Three incubating females took up to 3 dustbaths a day. The aerie of one incubating female who took regular dust baths in 1984 was heavily infested with swallow bedbugs (*Oeciacus vicarius*). The aerie was a large cave, and the chicks (4 of which fledged) probably were able to move away from the source of infestation.

On 28 May 1985 we saw a female Prairie Falcon drink water and take a bath in a depression in a rock, where water had collected after a rainstorm the previous day. Bent (U.S. Natl. Mus. Bull. 167:18–22, 1938) considered water bathing by Prairie Falcons a rare event. Captive Prairie Falcons, however, preferred water baths above dustbaths when both were provided (B. A. Haak, unpubl. data). The general scarcity of standing water in areas inhabited by Prairie Falcons may force them to take dustbaths, but apparently they prefer to bathe in suitable pools or puddles when available.

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express our thanks to G. T. Allen and S. V. Sherrod for their comments on an earlier draft. The research is a cooperative effort between Idaho Power Company, the Bureau of Land Management, Boise District's Snake River Birds of Prey Research Project, and Pacific Gas and Electric Company.—ANTHONIE M. A. HOLTHUIJZEN, *Idaho Power Company, Environmental Affairs Dept., Box 70, Boise, Idaho 83707,* PETER A. DULEY, JOAN C. HAGAR, SCOTT A. SMITH, AND KRISTIN N. WOOD, *Snake River Birds of Prey Research Project, Bureau of Land Management, 3948 Development Ave., Boise, Idaho 83705.* *Received 22 Apr. 1986, accepted 14 July 1986.*

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An incident of brood parasitism by the Verdin.—While in south Texas during May and June, 1980–1982, I recorded an incident of interspecific brood parasitism of a Northern Mockingbird (*Mimus polyglottos*) by the Verdin (*Auriparus flaviceps*), a species thought only to build its own nests.

On 22 May 1980, at the Val Verde Trailer Park, Donna, Hidalgo County, Texas, I found a Northern Mockingbird nest that contained two Bronzed Cowbird (*Molothrus aeneus*) eggs and a single Verdin egg, all of which were being incubated. The nest was located in a citrus tree, about 2 m above ground level. The eggs were taken by a predator about 24 hours after my discovery, before any hatched. To my knowledge, this is the first reported case of interspecific parasitism by the Verdin.

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Downy Woodpecker caches food.—Caching of food is rare in woodpeckers. Two species, the Acorn Woodpecker (*Melanerpes formicivorus*) (MacRoberts and MacRoberts, Ornithol. Monogr. 21, 1976) and the Lewis Woodpecker (*M. lewisi*) (Bock, Univ. Calif. Publ. Zool. 92, 1970) are known to store large numbers of acorns for future use. Food caching is also noted for the Red-bellied Woodpecker (*M. carolinus*), Gila Woodpecker (*M. uropygialis*), Golden-fronted Woodpecker (*M. aurifrons*), Red-headed Woodpecker (*M. erythrocephalus*), Hairy Woodpecker (*Picoides villosus*), and Red-bellied Sapsucker (*Sphyrapicus varius*), (Conner and Knoll, Auk 96:195, 1970, and references within). On 6 November 1985, I observed a female Downy Woodpecker (*Picoides pubescens*) feeding on poison ivy (*Rhus toxicodendron*) berries. The bird was about 3 m from me when first seen and moved to within 1.3 m as it foraged in a dying apple (*Pyrus malus*) tree. The bird sat crosswise on the twigs of both the poison ivy and apple, and often turned upside down in the manner of a Tufted Titmouse (*Parus bicolor*) or Black-capped Chickadee (*P. atricapillus*) to reach the ivy berries. Six times the bird flew, with one to several berries in its beak, to a second apple tree about 20 m away. On one occasion the bird was seen to place the berries in a crack in the bark

of this second tree. Although I could not determine whether caching occurred more than once, that this bird repeatedly carried ivy berries to the second tree and returned with an empty bill indicates that caching was the purpose of these trips.—ALBERT E. BURCHSTED, *Dept. Biological Science, College of Staten Island, 715 Ocean Terr., Staten Island, New York 10301.* *Received 21 Mar. 1986, accepted 18 June 1986.*

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ORNITHOLOGICAL LITERATURE

CURRENT ORNITHOLOGY. Vol. 2. By Richard F. Johnston (ed.). Plenum Press, New York, New York, 1985:364 pp., 43 numbered text figs., 26 tables. $41.00.—It is refreshing to find that one can pick up a book with a pretentious-sounding title and find the contents to be exactly as advertised. Not only do the chapters deal with some of the hottest (current) topics in ornithology, but these chapters are written by the established authorities in the respective fields. In the selection of some of the subjects for treatment, Johnston has shown elegant insight; in one case his choice of authors reveals subtle genius in his command of issues and the personalities involved, as I will argue below.

The book contains nine chapters. The first, entitled "Data Analysis and the Design of Experiments in Ornithology," by Frances C. James and Charles E. McCulloch, is worth the price of the book to experimental ornithologists. It is a clearly written, no-nonsense analysis of experimental models and hypothesis testing, and includes an appendix defining and explaining the important statistical techniques and terms used in analysis these days, and offering the pros and cons of each. The good news is that Popperian hypothesis testing (rejection of series of null hypotheses leading inexorably closer to the "truth") need not be the only valid approach to research. Indeed, the authors maintain strenuously, the art of inference is alive and well. Numerous areas of ornithological and other field investigations are not yet suited (for lack of maturity or precision) to the kinds of simple, unambiguous hypotheses that have been long used in molecular biology. Perhaps, after reading this article, young researchers will not feel so much pressure to pose simple, rejectable hypotheses that have no basis in the real world of nature.

Chapter 2 is an examination of "reversed" sexual size dimorphism in raptors by Helmut C. Mueller and Kenneth Meyer. In exploring the question of why female raptors are larger than males, the authors pose a series of reasonable hypotheses, rejecting most of them on the basis of data available in the literature on Palaearctic raptors. They correctly point out that diet per se can just as easily be an effect as a cause of this dimorphism. Other traits, such as colonial nesting and clutch size, are correlated with dietary habits. Female dominance during the breeding season is the life history trait most consistently correlated with reversed sexual dimorphism, and the authors conclude that it was a main factor in the evolution of RSD by "facilitating and maintaining the pair bond." As is usual with inferential studies, the reader should examine the assumptions carefully, but this thesis seems to be very carefully thought out.

Chapter 3 is a remarkable treatment of vocal "dialects" in White-crowned Sparrows (*Zonotrichia leucophrys*), remarkable not only because it clarifies most of the confusion in this area of study, but also because its authors include most of those now active in researching dialect phenomena and epiphenomena in this species. Donald Kroodsma originally wrote the article, and invited M. C. Baker, L. F. Baptista, and L. Petrinovich to amend it. These latter three represent different points of view, and it is instructive to read the points on which they agree. In this chapter it is pointed out that much of the confusion about the facts and effects of white-crown dialects results from the very different approaches and assumptions made by the various authors. Indeed, in any two papers on the subject, the parts of the song used as dialect markers will likely be quite different. Kroodsma et al. point out that the research questions and techniques of the main workers differ, that very real differences in basic demographic data can be obtained from different *nuttalli* populations, and that it is premature to make cause-and-effect conclusions about the correlations between demographic and vocal data. Given what some of these authors themselves have claimed

over the years, it is a real service to ornithology to have these valid differences openly discussed, and the necessary direction of future research identified. This is "must reading" for everyone interested in vocalizations.

Chapter 4, by G. F. Barrowclough, N. K. Johnson, and R. M. Zink, is about genic variation in birds, and focuses attention on the mutation-drift theory of genic variation. They maintain that electrophoretic variations (genetic variation expressed as protein variations identified through the technique of electrophoresis) should be considered as selectively neutral unless or until the data cause rejection of this model. Genetic data are notably poor for birds, and a great amount of new data must come to light before we can deal effectively with the question of the significance (such as behavioral-ecological and systematic) of genetic variation in birds.

Chapter 5, "Ecomorphology," by Bernd Leisler and Hans Winkler, is an attempt to shed light on the problem of the relationship between body form and ecology using a comparative approach with related species sharing similar lifestyles. For example, in a group of eight turdid chats that feed on arthropods on the grasslands of East Africa, the authors make extensive use of principal component analysis of morphological characters and ecological and behavioral data. The approach then reduces possible noise in the analysis by focusing on related species with somewhat similar lifestyles. The resulting ordinations amount to quantitative reassurance of many points that functional morphologists have made. For example, cursorial chats that dash after prey have longer tarsi and larger feet than those that more commonly pounce from a grass-stem perch. In a different group (six *Acrocephalus* warblers) a combination of discriminant analysis and principal component analysis helps the authors conclude that a rounded wing that confers maneuverability is of little importance in explaining habitat differentiation in the genus, while a combination of characters associated with clinging ability is useful. The authors are careful to point out the limitations of their approach, given the limited data available. They argue that more functional morphological and ecological work is needed, rather than more sophisticated analyses, and that future research in ecomorphology may lead in different directions than the current approach.

Chapter 6, "Problems in Avian Classification," by Robert J. Raikow, is a stimulating review and discussion of some of the upheaval in systematic biology. In an admittedly partisan statement, Raikow asks, "Why don't we have a satisfactory classification of the birds?" and reviews the strengths and weaknesses of the various techniques. These are the phenetic (numerical taxonomy), cladistic (phylogenetic or geneological), and traditional or eclectic (a combination using both similarities and descent) schools. Only the latter two have been used often in avian classification. If you have found ornithological classifications to be arbitrary and confusing, you will agree with Raikow that only cladistic, or evolutionary classifications make sense now that we have data from a variety of approaches, ranging from bones and behavior to DNA.

Chapter 7, "Syringeal Structure and Avian Phonation," by A. S. and S. L. L. Gaunt, is a remarkable review of the state of the art, and perhaps could be entitled, "All you thought you knew is in doubt, and much is plain wrong or simply unknown." Briefly put, the syrinx is buried deep in the thorax and difficult to work with. It is also variable from group to group. Given the diversity of syringes and models pretending to account for avian sound production, one hardly wonders that we have yet to arrive at the best questions. This article is an excellent statement on what is actually known about sound production and syringeal function (not very much) and what we have to learn before we can ask some relevant questions (a great deal).

Chapter 8, "Assessment of Counting Techniques," by Jared Verner is "must" reading for anyone who needs to count birds. It is a critique of the various techniques, and catalogs many misapplications of them. Verner states that most calculations of species diversity and

community energetics are suspect simply because the counting techniques on which they were based are demonstrably deficient. All is not without hope, however, as Verner thinks that certain goals, such as population trends, do not require the counting rigor that the above require. Overall, thoroughly executed spot counts should suffice for most applications, as long as larger areas than usual are sampled and much more time than usual is spent in the field. But even the accuracy of this method needs to be verified by application of total mapping of populations of marked birds, such that the importance of "floaters" can be determined. This article, and one on which it is based (to be published elsewhere), should have considerable impact on population assessment, though we probably can never circumvent some of the variation and biases in bird counting.

The final chapter, "Circadian Organization of the Avian Annual Cycle," by A. H. Meier and Albert C. Russo, reviews the interactions of external and internal timing factors. The annual cycle includes photoperiodism, photosensitivity, photorefractoriness, migratory restlessness and orientation, premigratory fattening, and egg laying. This article reviews the involvement of daily rhythms at the cellular and organ levels in these annual cycles. Many important details remain unknown, making an understanding of the interactions especially difficult. Evidence of circadian rhythms is found at all levels, and it is clear that the neuroendocrine system organizes and synchronizes them so that the entire animal responds appropriately to external rhythms. This chapter is only a partial list of such happenings, but it should make field ornithologists aware of the complexity of internal events leading to the well-tuned bird that breeds, molts, and migrates at the right times, managing not to get confused by annual and latitudinal variations in external environmental signals.

In summary, "Current Ornithology" contains the most up-to-date information from some of the most important areas of ornithology. It is clearly written by and for professional biologists, and should be in any well-appointed university or office library. Its usefulness to the amateur ornithologist may be limited, depending on the extent of background and motivation of the reader. The production of the volume is very good, with grammatical errors and typos being limited to Chapter 5, and these may be the fault of a translator. As review books go, the value for the price is much greater than some other recent volumes on birds by another publisher. Serious ornithologists should have this book, its predecessor, and probably subsequent volumes.—Curtis S. Adkisson.

Avian Monogamy. By Patricia Adair Gowaty and Douglas W. Mock (eds.). Ornithological Monographs No. 37, American Ornithologists' Union, Washington, D.C., 1985:vi + 121 pp. $11.00 ($9.00, members).—This "monograph" is based on papers given in a symposium on avian monogamy at the 1982 A.O.U. meeting at the Field Museum in Chicago. It consists of an introduction and seven chapters by symposium participants. Because neither the title of the volume nor its advertisements provides information about its contents, the major function of this review is to present brief abstracts of the chapters.

I would first, however, like to express a negative reaction to the use of the A.O.U. monograph series to publish what, in my opinion, amounts to an essentially miscellaneous collection of papers. The papers do share the commonality of dealing to some extent with monogamy (as did eight other symposium papers not published here), but I cannot see that the papers are linked to one another in any way that makes their joint publication more desirable than their publication as separate articles. Indeed, there are reasons for believing that their publication as journal articles would have been of greater service to the authors and their potential audience. When published in a major journal a paper receives immediate, worldwide distribution to several thousand individuals and libraries (at a prepaid cost) and, typically, subsequent additional distribution via reprints (for postage costs). As a chapter in

this monograph, a paper may be immediately distributed to only a couple of hundred individuals and libraries, and finally achieve a distribution of perhaps 500 original copies. To be sure, it is likely that all interested persons will eventually learn of these articles and gain access to them (at extra cost), but "eventually" is less than satisfactory. Many persons whose research or writing could benefit from knowledge of one of these articles at the time of its publication may not learn of its existence for more than a year when a review or a listing in a reference service finally appears. In short, publication in the monograph series delays the spread of knowledge of the existence of these papers, and also results in their being more difficult and costly to obtain. I believe authors and audiences alike would be served better by the A.O.U. Monograph series if it were used as intended "for major papers too long for inclusion in the Union's journal, 'The Auk'" (see p. ii, this monograph), and perhaps also when there really is something to be gained by having a collection of papers together in one volume.

Now, about the component chapters, the "Introduction" by Mock is a brief statement of some of the interesting questions about the evolution of monogamy together with some suggested directions for future research.

The second chapter by Gowaty, "Multiple Parentage and Apparent Monogamy in Birds," is based on her studies of kinship in families of Eastern Bluebirds (*Sialia sialis*) in which she discovered examples of broods having multiple paternity and maternity. Although it is still not known how widespread are the behavioral patterns that produce broods of mixed paternity-maternity, the evidence is mounting that they are not uncommon. If that proves to be the case, Gowaty suggests that our concept of mating systems may have to be changed from one based on male-female association patterns to one based on genetically effective matings.

Chapter 3 by Nancy Burley is entitled "The Organization of Behavior and the Evolution of Sexually Selected Traits," and focuses on the problem of how sexual dimorphism can arise within a monogamous system. Burley presents results of several sets of experiments with captive Zebra Finches (*Poephila guttata*) that appear to demonstrate preexisting preferences in both sexes for novel phenotypes of both the same and the opposite sex. To explain such preexisting preferences she postulates the existence of evolved plans for decision making that could account for the rapid evolution of sexually selected traits.

The fourth chapter, "Mate Preferences and Mating Patterns of Canvasbacks (*Aythya valisineria*)," by Cynthia K. Bluhm, reports on the importance of free mate choice for successful reproduction. In this experimental study of captive birds, eggs were laid only by the females of self-formed pairs; females of randomly assigned pairs not only did not lay, but often persisted in behaving aggressively toward their assigned mate.

Chapter 5 by Michael G. Anderson is entitled "Variations on Monogamy in Canvasbacks (*Aythya valisineria*)." Studies of wild, individually marked Canvasbacks revealed that male Canvasbacks are occasionally polygynous and only rarely engage in forced copulation attempts. More common is a secondary male strategy of engaging in extrapair courtship, which sometimes leads to serial monogamy.

Chapter 6, "Primary and Secondary Male Reproductive Strategies of Dabbling Ducks," by Frank McKinney, is an excellent review and synthesis of what is known about the mating patterns of members of the genus *Anas*. Although McKinney says that relatively few studies of either wild or captive members of this well-known genus have focused on variations in mating patterns, it is clear from this review that what studies have been done (many by the author and his associates) have been well employed to develop convincing hypotheses about the ecological and social factors that may favor certain variations (EPC, polygyny) on the basic *Anas* pattern of monogamy.

Chapter 7, "Adaptive Significance of Monogamy in the Trumpet Manucode (*Manucodia*

keraudrenii) (Aves: Paradisaeidae)," is by Bruce Beehler. This paper is an important original contribution to our understanding of how such factors as diet may affect the pattern of parental care and the mating system of a species. Beehler argues convincingly that the manucode's specialization on food (several species of figs) of low nutritive value and of unreliable abundance results in mandatory male parental care, and thus monogamy, in a species belonging to a family in which polygyny is the rule.

The eighth chapter, "The Influence of Demography on the Evolution of Monogamy," is by Bertram G. Murray, Jr. Murray points out that demographic phenomena such as longevity, annual fecundity, and sex ratios are often not given sufficient consideration as factors affecting the evolution of mating systems. Using hypothetical and real examples, he illustrates how expected longevity and fecundity may influence a female's choice of whether to breed with an already mated male or wait until next year for a chance to mate monogamously.

Although there is variability in the significance of the contribution of each chapter, all are of interest and worthy of publication. Unfortunately, this monograph is not a very good vehicle for their publication.—NORMAN L. FORD.

GUIDE DES PASSEREAUX GRANIVORES EMBERIZINÉS. By Gilbert C. Armani. Société Nouvelle des Editions Boubée, 11 Place St.-Michel, Paris 6e, France, 1985:416 pp., 28 color plates, appendices, index, bibliography. 230 francs (about $33.00).—"The information given in the text is the result of notes and research begun by my grandfather about 1880 and pursued as a family project during more than a century" (p. 11). But who was the author's grandfather, or who, for that matter, is the author himself? According to the inside cover, Gilbert C. Armani is an associate at the National Museum of Natural History in Paris. I confess that I have never heard of him, in spite of my having followed rather closely the developments of ornithology in France in the last 2 decades or so. The book is apparently the second of a projected three-volume set on the granivorous birds of the world. The first volume, published in 1983, dealt with the Fringillinae, Carduelinae, and Cardinalinae, and the third volume will include the Estrildidae, Viduinae, and Ploceidae. The present book, after a very brief introduction to the Emberizinae (pp. 17–20), consists essentially of the description of the 282 species included in the Emberizinae, largely following the order and nomenclature of Paynter and Storer in Peters' Check-List. The format is the same for each species: description, voice, habitat, distribution, behavior, nest, and subspecies and their distribution when applicable. The main part of the text (pp. 21–368) is followed by 28 color plates drawn by the author and illustrating all species; a table showing their distribution by geographical region and by country (pp. 369–390); a list of introduced species (pp. 391–392); an alphabetical list of French names and the corresponding Latin names (pp. 393–399); an alphabetical list of Latin names with their French and English vernacular equivalents (pp. 400–406); an index of Latin and French names (pp. 407–413); and a "brief bibliography" or rather, list of about 75 books, mostly faunal works and field guides, geographically arranged (pp. 414–416).

The author did not mention the intended audience of his book, but a flier included in the book states that it "addresses itself to the amateur ornithologist and also to the professional." The text does not contain any references to published works, and it is far from clear where, indeed, the information used for the text came from. Presumably, this book is a compilation of data included in the general texts cited at the end of the volume and of unpublished notes gathered by the author, who, it is stated, traveled widely to study Emberizinae. The lack of citations to the original literature sources or to the original field work will make the work useless for the professional ornithologist. The amateur cannot really use this book as a field guide because the descriptions are not written in field-guide fashion, and because the color

illustrations are not of the standard one is now accustomed to in field guides. Furthermore, not all plumages are depicted. Nor can the amateur rely on this text as a source of references on the emberizines because the factual basis is unknown. Finally, for both professionals and amateurs, I must admit that the absence of credentials of the author does not inspire confidence, even though it is possible that the compilation was done carefully (note here, however, that typos are common, especially in the bibliography). A number of excellent books on birds, both technical and popular, have been published in France recently. This volume is not one of them, and I cannot recommend it.—FRANÇOIS VUILLEUMIER.

CONSERVATION STUDIES ON RAPTORS. By I. Newton and R. Chancellor (eds.). International Council for Bird Protection, Cambridge, England, 1985:xi + 482 pp., numerous tables and figs. About $38.00.—This volume includes "main papers" presented at the Second World Conference on Birds of Prey held at Thessaloniki, Greece, in April 1982. The contents were "restricted to papers of scientific nature which present new material, together with a section of miscellaneous papers covering different management techniques." In my opinion, more than a few papers fail to meet these restrictions and would not be acceptable for publication in a refereed scientific journal. On the positive side, the entire volume is in readable English despite the fact that the more than 60 authors include individuals from nine countries where the native language is not English. Overall, the editors deserve praise for making the best of an impossible task. The book is divided into five parts, plus a section of 26 pages containing a summary of several "workshops" on vulture conservation. The latter is a list of participants and their interests, plus very brief summaries of the recent work of some of the participants.

Part I consists of 14 papers and 154 pages on the status and population declines of raptors in the Mediterranean region. Some of the papers offer little quantitative information, but the overall quality is good.

Part II consists of eight papers and 74 pages on tropical forest raptors, and primarily shows how little we know about these species. Populations are being severely reduced by the worldwide destruction of this habitat. The paper by Jones and Wahab Owadally on the Mauritius Kestrel (*Falco punctatus*) is obsolete and controversial in its analysis; the population has increased considerably in the past few years (S. Temple, pers. comm.).

Part III, "Migration of Raptors," contains 89 pages and 13 papers, which vary from poor to excellent. Most of the papers present counts of migrating raptors from one or more localities and some speculation about the sources, destinations, and routes, often without much basis. Some of the counts are astounding; for example, 764,000 raptors passed Eilat, Israel, in one spring, and 958,000 flew through the Isthmus of Panama in one autumn. The weakest paper is by Vagliano on raptor migration in Greece. It contains no data and speculates that raptors use hypothesized migration routes because of the influences of geomagnetism, paleohistory, and minute differences in the geographic distribution of gravitational forces. Another strange inclusion is the paper by Kirkwood on food requirements for the deposition of energy reserves. Although I have no arguments with the hypotheses and calculations, no data are presented, and I wonder what it tells us about raptor migration or conservation. Readers should note that Evans and Rosenfield "suggest" that female Sharp-shinned Hawks (*Accipiter striatus*) winter farther south than males, but their results are not statistically significant. (I have heard their results quoted as proof.) Shelley and Benz found that 8% of migrating Broad-winged Hawks (*Buteo platypterus*) at Hawk Mountain, Pennsylvania, had distended crops, suggesting that this species frequently feeds during migration. They neglect to note that their sample may be biased. First, they were able to examine only 6% of the individuals observed, only those birds seen in profile, and hence flying low. Feeding individuals are certainly overrepresented in this sample. Second, 1981 was a very

poor year for observing migrants at Hawk Mountain, and it is possible that those migrants flying low enough to be seen were the individuals that had been unable to acquire sufficient energy reserves for migration, or that the unusual weather conditions slowed the southward progress of migrants and increased the incidence of feeding behavior. Smith, in what I believe is the best paper in this part of the book, presents compelling arguments for a lack of feeding by Broad-winged Hawks and Swainson's Hawks (*B. swainsoni*) during migration; the latter probably does not feed for the 2 months it takes to soar from the Great Plains to the Pampas.

Part IV, "The Peregrine Falcon," contains 8 papers and 65 pages and is severely dated. Papers presented at the International Peregrine Conference in November 1985 render most of this section obsolete. Let us hope that we will not have to wait more than three years to see these papers in print.

Part V, "Management and Conservation," contains 9 papers and 61 pages. Topics include monitoring birds with color bands through telemetry, supplemental feeding, and captive breeding and cross-fostering. This part contains some biological information on mortality rates. The best paper is a brief yet thorough review of telemetry techniques by Kenward; the least useful is by Platt on the captive breeding of falcons for falconry in Bahrain.

Overall, this volume is of interest only to those who are curious about the population status of raptors and in management and conservation techniques in various parts of the world. There is little of interest for the "pure" raptor biologist, and even less for an ornithologist with no special interest in the birds of prey. The high price will also help keep the book off of the shelves of private and institutional libraries.—HELMUT C. MUELLER.

OCCUPATION OF URBAN HABITATS BY BIRDS IN PAPUA NEW GUINEA. By Harry L. Bell. Proceedings of the Western Foundation for Vertebrate Zoology, Vol. 3, No. 1, February 1986:48 pp., 1 map, 9 tables, appendix. $7.00.—Harry Bell, who died before this paper was published, was a dedicated amateur who, given the time and encouragement, not only made a significant contribution to the literature, but also was able to create a fulfilling second career as a full-time student of Australasian ornithology by obtaining his doctorate at a time in life when most people are beginning to think of retirement. This work is another example of Harry's dedication to the ornithology of Papua New Guinea—the independent "eastern New Guinea" that also includes the Bismarck Archipelago and two northernmost Solomon Islands.

This paper on urban bird communities in Papua New Guinea addresses a curious topic about which we have very little information. This is no surprise, as most ecologists who work in the humid tropics are short-term visitors, spending as much time as possible in forest habitats far from urban areas. Thus, in the quest for "pristine" forest study sites and the pursuit of studies related to rain-forest biotas, most researchers overlook the potentially significant events taking place in modern tropical towns and cities.

Ornithologically, what happens when a city is carved out of the forest? Which species become the familiar songbirds of downtown and backyard? Such questions are particularly interesting in the context of the Papuan region, because it is almost entirely free of the well known urban commensals such as House Sparrow (*Passer domesticus*), European Starling (*Sturnus vulgaris*), Rock Dove (*Columba livia*), and Common Myna (*Acridotheres tristis*).

To the average reader, any general patterns that may link the 14 urban study populations examined in this paper are perhaps obscured by the details of an unfamiliar avifauna and many peculiar distributions. Nonetheless, two trends, well-known for other tropical regions, are documented for Papua New Guinea: (1) the dominant urban species tend to be nonforest or forest-edge forms, and (2) widespread lowland species often colonize upland areas sub-

sequent to man-related clearance of the forest. In the instance of the Lemon-bellied Flycatcher (*Microeca flavigaster*), typically a lowland savanna species, one can only wonder how this bird has managed to colonize the isolated and far-flung highland valleys from which it is now known.

Bell found strong regional differences in the composition of Papuan urban avifaunas. Such is immediately obvious to any birder who visits, for example, four of the more important "mainland" communities—Port Moresby, Lae, Mount Hagen, and Madang. Each town supports a set of "common" species that differs considerably from any other. Some of these differences can be explained by habitat or altitude (e.g., Port Moresby is in a belt of coastal savanna, Mount Hagen is 5000 ft higher than Lae), but most seem to relate to history of colonization. Even neighboring towns (Wau and Bulolo) show striking differences. To this, add the point Bell makes concerning the dynamic nature of these relatively "new" bird communities, and the reader can see that a splendid natural experiment is presently in operation. One of the main points is that the data presented in this paper will serve as a well-documented benchmark for comparison one or two decades hence. It is unfortunate that Harry Bell won't be here to ensure that the follow-up work is done with equal thoroughness.—Bruce M. Beehler.

Arizona Wetlands and Waterfowl. By David E. Brown. Univ. Arizona Press, Tucson, Arizona, 1985:169 pp. 70 numbered figs., 9 tables, 7 colored plates, and 18 maps in an appendix. $24.95.—This attractive book summarizes in very readable form the results of over 30 years of research by biologists from the Arizona Game and Fish Department, U.S. Fish and Wildlife Service, and various universities. A Game Branch Supervisor with the Arizona department, Brown presents a thorough description of the state's major wetlands and the more than 30 species of Anatidae recorded in an area most associate with deserts. Basic biology, taxonomy, anatomy, foods, and diseases are covered, as are specific management approaches.

Although the species accounts repeat some facts found in standard works on waterfowl, such as "Ducks, Geese and Swans of North America" by F. C. Bellrose, they include much "local color" and many details on distribution, historical and present, as well as breeding biology and responses to hunting and habitat changes. Distribution and migration are well described in text and maps. The sections on the whistling ducks and the Mexican Duck (*Anas platyrhynchos diazi*) are especially interesting, as many data are included from theses and agency reports that are not readily available.

Bonnie Swarbrick Morehouse, author of a M.S. thesis on the Mexican Duck, illustrated the text with many outstanding black-and-white sketches. The seven full-page color paintings of waterfowl, however, are a bit gaudy and appear flat in the copy I reviewed.

Few errors were noted, but one habitat photo caption mentions "the emergent aquatic waterweed (*Anacharis canadensis*) . . ." when the only obvious emergent seems to be a smartweed (*Polygonum* spp.). The book is well written and carefully edited. I recommend it highly, particularly to anyone interested in this fascinating area and the fascinating waterfowl it harbors.—Ronald A. Ryder.

Blackbirds of The Americas. By Gordon H. Orians, illus. by Tony Angell. Univ. Washington Press, Seattle, Washington, 1985:164 pp., 82 pen-and-ink drawings, charts, maps, 2 appendixes, selected references, and index. $24.95.—For 25 years Gordon Orians has published scientific works on various aspects of blackbird biology. Now Orians has summarized

the results of decades of research on icterids in a beautifully illustrated and extremely readable book that explains his fascination for this family of birds.

"Blackbirds of The Americas" is written primarily for the nonprofessional, although it contains a wealth of information on subjects such as geological and climatic influences, anatomy and systematics, and behavior and ecology. Despite the nontechnical focus of the book, I enjoyed reading it, and I appreciated the author's attempt to teach, in a gentle and effective way, the reality of the scientific method. Throughout the book, Orians demonstrates the proper use of hypothetico-deductive scientific inquiry, and in the last chapter he gives the following apt description: "Science . . . requires the ability to hold ideas and images in our heads in the absence of the real thing, an ability to play with these ideas intellectually, and an ability to conceive of tests of those ideas. Scientific methods are nothing more than a set of rules about how to deal with hypotheses. The most important impact of the rules is that they help us devise tests that could falsify a hypothesis that is wrong. We all develop identities with our ideas and would prefer them to be correct rather than incorrect. To counter this bias, which might cause us to seek only favorable evidence, we need the discipline of rules."

In his attempt to summarize research on blackbirds, and to illustrate hypothesis testing, Orians presents the results of selected studies in an informal and engaging way. Although he attempts to demonstrate some of the inconsistencies and differences that seem to be inherent in research, Orians does not provide a complete review of the huge blackbird literature, nor does he provide a complete list of references. A reader whose interest is sparked by Orians's vivid descriptions, however, could easily use the references listed for each chapter to discover the complexity and intrigue produced by blackbirds and their researchers.

Tony Angell's beautiful black-and-white illustrations are remarkably detailed, and they richly supplement Orians's written descriptions. In a few sections such as color differences between the sexes, the role of color in communication, and variation in plumage with age and sex, I would have appreciated the addition of color photographs, but the lack of them is not serious and reduces cost.

I would recommend "Blackbirds of The Americas" to anyone with an interest in birds. This book is also an extremely interesting and readable account of the real world of science and scientists. Gordon Orians holds a special place in my scientific heart, and as I start the 14th field season of my own quixotic quest to understand the Red–winged Blackbird (*Agelaius phoeniceus*), perhaps Orians's favorite icterid, this book helps me understand why so many are fascinated by blackbirds.—KEN YASUKAWA.

THE AUDUBON SOCIETY GUIDE TO ATTRACTING BIRDS. By Stephen W. Kress, illus. by Anne S. Faust. Charles Scribner's Sons, New York, New York, 1985:377 pp. $24.95.—At a time when there are probably more publications available on attracting birds than at any time past, one wonders why an author would write another book on the topic. However, Stephen Kress's comprehensive effort, "The Audubon Society Guide to Attracting Birds," offers several things hard to find in most books on attracting birds. The guide offers many ideas on attracting birds to large properties, such as farms and ranches, as well as backyards. Ideas suitable for wooded yards in the East are found in many books, but Kress expands on this theme to include improvement of properties in dry, open habitats, such as desert dwellings and prairie ranches. He includes ideas on providing dependable sources of water for wildlife in dry country, nest sites for larger birds, and plantings suitable for all sections of North America. The guide provides an annotated list of native plant species useful for landscaping and attracting birds. More than 200 drawings by Anne S. Faust show the form,

fruit, and leaves of selected plants, and tables provide information on many others. Kress also gives an annotated list of mail-order nurseries, sources for native plants, and bird-attracting products. This list alone might be worth the purchase price of the book for many readers, as many plants recommended by Kress and other authors are hard to find. The catalogues of these suppliers will provide many additional ideas. The chapter on pools and ponds provides designs and plants suitable for various situations and suggestions for management of ponds. There is a good chapter on supplemental feeding, and an annotated list of references including a state-by-state list of publications that should provide ideas for any place in the country. Kress writes for the general reader. Technical terms are defined and many plans and drawings provide adequate illustration for hundreds of interesting bird-attracting devices and landscaping ideas.—ALBERT R. BUCKELEW JR.

CATESBY'S BIRDS OF COLONIAL AMERICA. By Mark Catesby, edited by Alan Feduccia. Univ. North Carolina Press, Chapel Hill, North Carolina, 1985:176 pp., 20 color plates, 110 black-and-white plates, 2 facsimile pages, 1 map. $24.95.—Mark Catesby's "The Natural History of Carolina, Florida, and the Bahama Islands" was first published in 1731–1743. The pre-Linnean, bilingual work (French and English), which included 220 color plates as well as a lengthy text, established Catesby at once as the preeminent natural historian of colonial North America. It also ensured him his place as the founder of American ornithology. But, although the book was well received in Europe, only three copies were sold in America, and Catesby's work fell into obscurity in the 19th century, when it was eclipsed first by Alexander Wilson's "American Ornithology" and then by John James Audubon's "Birds of America." The current offering, a "lightly edited" text of Catesby's work, accompanied by 20 color plates as well as black-and-white illustrations of all 109 "species" of birds described by Catesby, is a long overdue attempt to reacquaint professional and amateur ornithologists with this important historic figure. Although purists may question the value of a lightly edited text, the result is an easy to read account of Catesby's travels in colonial America. Editor Alan Feduccia has arranged the black-and-white plates in the approximate order that the birds appear in the current A.O.U. Check-list (sixth ed.). Each is accompanied by Catesby's text for the plate, as well as by a separate brief "update" on the species by Feduccia. This method of presentation works well, and enables the reader to administer the volume in either large or small doses. One engaging, albeit likely unintentional, result of the arrangement is that it offers the reader an opportunity to guess at what Feduccia is about to point out.

Catesby's text is, of course, hopelessly out-of-date; but although many of his "errors" seem rather comical in light of 20th-century ornithological knowledge, others are strikingly cautionary. For example, after having described the White and Brown curlews (the adult and juvenile White Ibis [*Eudocimus albus*], respectively) as separate species, he notes that the "near resemblance in them made me suspect they differed only in sex, but by opening them, I found testicles in both kinds." Thus an inappropriate assumption nullified the scientific method in the 18th century just as forcefully as it does now. On the other hand, Catesby's text provides numerous examples of "lost" knowledge. He correctly describes, for example, the hover-hunting behavior of Ospreys (*Pandion haliaetus*), right down to their success rates (it ". . . seldom rises without a fish . . .") and vulnerability to piracy (". . . the bald eagle (which is generally on the watch) no sooner spies [the Osprey] but at him furiously he flies . . . soars above him, and compels the hawk to let it (the prey) fall . . ."). He also debunks the then widely held notion that many birds spend the winter in torpor in caves or hollow trees: "If the immenseness of the globe be considered, and the vast tracts of land remaining unknown but to its barbarous natives, it is no wonder we are yet unacquainted

with the retreats of these itinerant birds." While speculating on how "European" birds found their way to America following their release from Noah's Ark, Catesby at first hesitatingly evokes dispersion as an explanation for current avian distribution before begging the reader to consider a vicariance explanation based on continental drift!

Prophetically, his descriptions of "the pigeon of passage" (Passenger Pigeon [*Ectopistes migratorius*]) and "the largest white-bill wood-pecker" (Ivory-billed Woodpecker [*Campephilus principalis*]) include references to fatal contact with man.

Catesby also covers a number of non-ornithological topics, including how to pickle sturgeon and make caviar, how to derive pitch and tar from pine, and why not to hunt deer Indian-style.

While I disagree with several of the editorial comments—but afterall, an editor's comments seem destined to evoke at least some grumbling—I congratulate Alan Feduccia for his yeoman effort. American ornithologists can no longer claim unavailability as an excuse for not having read Catesby. The first "profusely" illustrated tome on America's birds should be on every ornithologist's night stand.—K.L.B.

Birds, Men and Books. A Literary History of Ornithology. By Peter Tate. Henry Sotheran Ltd., London, England, 1986:193 pp. 20 black-and-white photos. £13.95.—After having consulted "The Handbook of British Birds" have you ever wondered just who that imposing set of authors, Witherby, Jourdain, Ticehurst, and Tucker, was? This book might help you find out, and the information you get might be accurate. But then again it might not. The author proposed to write a history of bird books, which for many years also was a history of ornithology. Of course, only English language books and Anglographic authors are discussed. Although most of these are British, a fair assortment of Americans, as well as two Australians and one New Zealander, are mentioned. The coverage of the present-day writers is almost exclusively British, the only Americans being Nice, Sutton, and Peterson.

The history essentially starts with William Turner, although there is some mention of earlier work, and proceeds through Willughby and Ray, White, Audubon, Gould, Sharp, Baird, and ends up with such people as Peterson, Lack, Fisher, and Sutton. There are accounts, variable in length, of the life and contributions of these people, and subjective evaluations of their work. One of the little gems that will amuse and startle young academics striving for tenure is the comment that in the 18th century the Oxford professor of botany held his chair for 36 years during which time he published no scientific work and gave only one lecture. A number of photographs of some of the more important people grace the book.

The biographical sketches, mostly anectodal and highly superficial, were obviously gleaned from more thorough sources. A very limited bibliography of only 27 entries is included, and no references are cited for any statement.

I am unable to comment on the accuracy of statements made about the British authors, but inaccuracies or distortions abound in the accounts of the Americans. For example, Audubon's travels are not accurately described, and the discredited idea that Audubon studied under the French artist David is again brought forth. The charges of libel and blackmail made against the young Alexander Wilson were not made "—on some trumped up and unreliable evidence—" (though members of this Society might wish that to be true). The Arthur A. Allen Medal is not given by the A.O.U. None of these errors is especially important, but their number casts doubt on the whole work.

Besides these distortions and outright errors, there are many examples of sloppy editing or plain carelessness on the part of the author. For example, on p. 119 the name of Margaret Morse Nice's husband is given as "Leonard B. Morse." A number of names are mispelled:

Tavener (p. 168 = Taverner), Sewell (p. 169, 189 = Sewall). The author seems unable to cope with the passage of years in a mathematical sense. On p. 169 we are told that G. M. Sutton went to The University of Michigan in 1947 and spent 14 years there. Later in the same paragraph we are told that he left Michigan for Oklahoma in 1952. On page 153 we are told that Reg Moreau published his treatise on Palaearctic-African migrations in 1972, two years before his death, which according to p. 154, occurred in 1970.

In summary, one can enjoy the stories told here, but one cannot rely on their accuracy. A publisher's ad for the book, which I have seen, expresses the opinion that "This book will become the standard work." I would hope that it does not.—GEORGE A. HALL.

JOHN XANTUS: THE FORT TEJON LETTERS. By Ann Zwinger. University of Arizona Press, Tucson, Arizona, 1986:xxvi + 255 pp., 2 black-and-white photos. $23.50.—John Xantus has always been an enigmatic figure in American ornithology, a compulsive liar who joined the army under an assumed name and a contentious charlatan who apparently could get along with no one, but for all of that a superb field collector and observer. From April 1857 to January 1859 he was a hospital steward in the army post of Fort Tejon, California, a position apparently obtained for him by S. F. Baird of the Smithsonian Institution. During that period he sent back to the Smithsonian some 2000 bird specimens of 144 species as well as quantities of other zoological and botanical material. He was a prolific letter writer and we have at hand a transcription of 49 of his letters to Baird written during his stay at Fort Tejon.

Ms. Zwinger has transcribed and annotated these letters, which present an informative picture of the southern California area in the 1850s. The annotations often quote from Baird's letters to Xantus and also give us an insight into other people and conditions of that time. She also attempts to translate the nomenclature of the period to that of today. In this last effort Ms. Zwinger has been generally successful, although I noted an occasional mistake. Her possible lack of biological knowledge shows occasionally as, for example, when she (mistakenly) explains that Xantus' references to "grizzlys" refers to the common Black Bear (*Ursus americana*).

A lengthy introduction gives a brief biography of Xantus both before and after his California sojourn. An appendix gives a list of the bird species found by Xantus using both his names and the present-day ones.

This is a useful addition to any collection of works on ornithological history.—GEORGE A. HALL.

BIRD CONSERVATION. 2. By Stanley A. Temple (ed.). Univ. Wisconsin Press, Madison, 1985:180 pp. $12.95.—The second annual number of this publication of the United States Section of the International Council of Bird Preservation is devoted to island biology. The principal articles are: "Why endemic island birds are so vulnerable to extinction" by Stanley A. Temple; "Historical and current factors affecting Hawaiian native birds" by C. John Ralph and Charles Van Riper III; "Distribution and abundance of Hawaiian native birds" by J. Michael Scott and Cameron B. Kepler; "Endangered birds in Micronesia: Their history, status, and future prospects" by John Engbring and H. Douglas Pratt; and "Bird conservation in the United States Caribbean" by James W. Wiley. There are short papers on Peregrine Falcon (*Falco peregrinus*) restorations and California Condor (*Gymnogyps californianus*) recovery efforts as well as a review of Bird Conservation Literature.—GEORGE A. HALL.

THE NATURALIST'S FIELD JOURNAL. By Steven G. Herman. Buteo Books, Vermillion, S.D., 1986:vii + 200 pp. 1 photo. $14.00 (paper).—The author has prepared a "Manual of Instruction based on a system established by Joseph Grinnell." A list of equipment, as well as detailed instructions (down to how to fill the technical pen) and a number of sample pages from the author's own journals are given. I expect that every experienced field worker has long since adopted his own system of keeping notes, but I recommend that all professors keep a copy of this book on hand for beginning graduate students to read.—G.A.H.

Wilson Bull., 99(1), 1987, pp. 150–152

ANNOUNCEMENTS

SYMPOSIUM ON FOOD EXPLOITATION BY TERRESTRIAL BIRDS

A symposium on food exploitation by terrestrial birds will be held at the Asilomar Conference Center, Pacific Grove (Monterey), California, on 19 March 1988. The symposium will be held in conjunction with the 58th Annual Meeting of the Cooper Ornithological Society. The intent of this symposium and subsequent published proceedings is to bring together for presentation and discussion scientists involved with the design and analysis of studies exploring how birds exploit food resources. Topics must be limited to nonraptorial, terrestrial birds. *Abstracts, due 1 March 1987,* are solicited that review the particular subject area as well as presenting new data. The symposium is being organized by Michael L. Morrison, C. John Ralph, Jared Verner, and William M. Block, with sponsorship from several private, state, and federal organizations. For instructions on submission of abstracts, and other information on the symposium, write: Michael L. Morrison, Dept. Forestry and Resource Management, Univ. California, Berkeley, California 94720. Phone: 415/642-5344.

1987 ANNUAL MEETING OF COLONIAL WATERBIRD SOCIETY

The 11th Annual Meeting of the Colonial Waterbird Society will be held at the Red Oak Inn in Thunder Bay, Ontario, 10–13 September 1987. Lynn Hauta and John P. Ryder are in charge of local arrangements. Announcements of the schedule and call for papers will be mailed to members at a later date.

AVIAN FAMILY-GROUP NAMES

The Standing Committee on Ornithological Nomenclature of the International Ornithological Committee has prepared a list of established names of avian family-group taxa (subtribes to superfamilies) and their synonyms as the first step in the process of writing an application to the International Commission on Zoological Nomenclature to stabilize use of these names. The SCON wishes to obtain input from all interested ornithologists and zoologists on this list of avian family-group names and its proposed application to the ICZN. The list is available to all interested ornithologists and zoologists who are willing to examine

it carefully and provide the SCON with corrections, additions, comments, and suggestions. This list of avian family-group names is unofficial and should not be used for any purposes other than that just mentioned. Copies of the list may be obtained by writing to Professor Walter J. Bock, Chairperson SCON; Dept. Biological Sciences, Columbia Univ., New York, New York 10026, USA.

WANTED: ITEMS FOR POSSIBLE USE FOR THE CENTENNIAL CELEBRATION OF THE WILSON ORNITHOLOGICAL SOCIETY

In 1988, The Wilson Ornithological Society will celebrate its first 100 years. As part of the celebration activities, a history of the Wilson Society is being prepared. We are most anxious to examine papers, photos, or other materials that would be useful in preparation of that history.

At the Centennial meeting we will have a display of items of historical interest to the society such as old photos, letters, art work, advertisements, banquet favors, etc. The WOS once even had an official lapel pin. Does anyone have one?

If you have items that are of potential use in preparation of our history or the Centennial display, please contact: Jerome A. Jackson, Chairman, WOS Centennial Committee, Box Z, Mississippi State, Mississippi 39762.

WANTED: COPIES OF *THE WILSON BULLETIN*

The Environmental Sciences School of the National University of Costa Rica is setting up the first graduate wildlife management program in Latin America with assistance from World Wildlife Fund-US (WWF-US); the United States Fish and Wildlife Service, International Affairs Office (USFWS); and the Organization of American States (OAS), among other organizations. The program, which is similar to a North American graduate program and leads to a Master's Degree in Wildlife Management, is scheduled to begin in February 1987 with 12 students from Central and South America. Four foreign professionals will be assisting the program during the first three years as visiting professors. Emphasis will be broad based and focus on endangered, nongame, and pest species, and on the management of genetic resources and systems in tropical environments. Students will work closely with human communities and government organizations during their three-year training period.

Over the past two years the program has been able to accumulate a respectable collection of wildlife related materials that presently includes nearly 300 book titles, over 5,300 reprints, approximately 700 non-periodical documents, and incomplete collections of 17 scientific journals. The center is pleased to report that previous appeals have resulted in the donation of Volumes 83–96 of *The Wilson Bulletin.* The coordinators of the program are particularly interested in completing the collection and ask members of the Wilson Ornithological Society for donations of numbers prior to Volume 83, as well as for back issues of other ornithological journals and books in the field. Donations should be sent in boxes weighing less than 40 pounds to Herb Raffaele, Office of International Affairs, U.S. Fish and Wildlife Service, Washington, DC 20240. All donations will be formally acknowledged by the wildlife program.

Christopher Vaughan, University Coordinator
Stephen E. Cornelius, Regional Coordinator

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The Wilson Bulletin

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See Wilson Bulletin, 98:335–336, 1985 for more detailed "Information for Authors."

Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Sixth Edition, 1983) insofar as scientific names of U.S., Canadian, Mexican, Central American, and West Indian birds are concerned. Abstracts of major papers should be brief but quotable. In both Major Papers and Short Communications, where fewer than 5 papers are cited, the citations may be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (AIBS, 1983). Photographs for illustrations should have good contrast and be on glossy paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

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Membership Inquiries

Membership inquiries should be sent to Dr. Richard Stiehl, Department of Biology, Southeast Missouri State Univ., Cape Girardeau, Missouri 63701.

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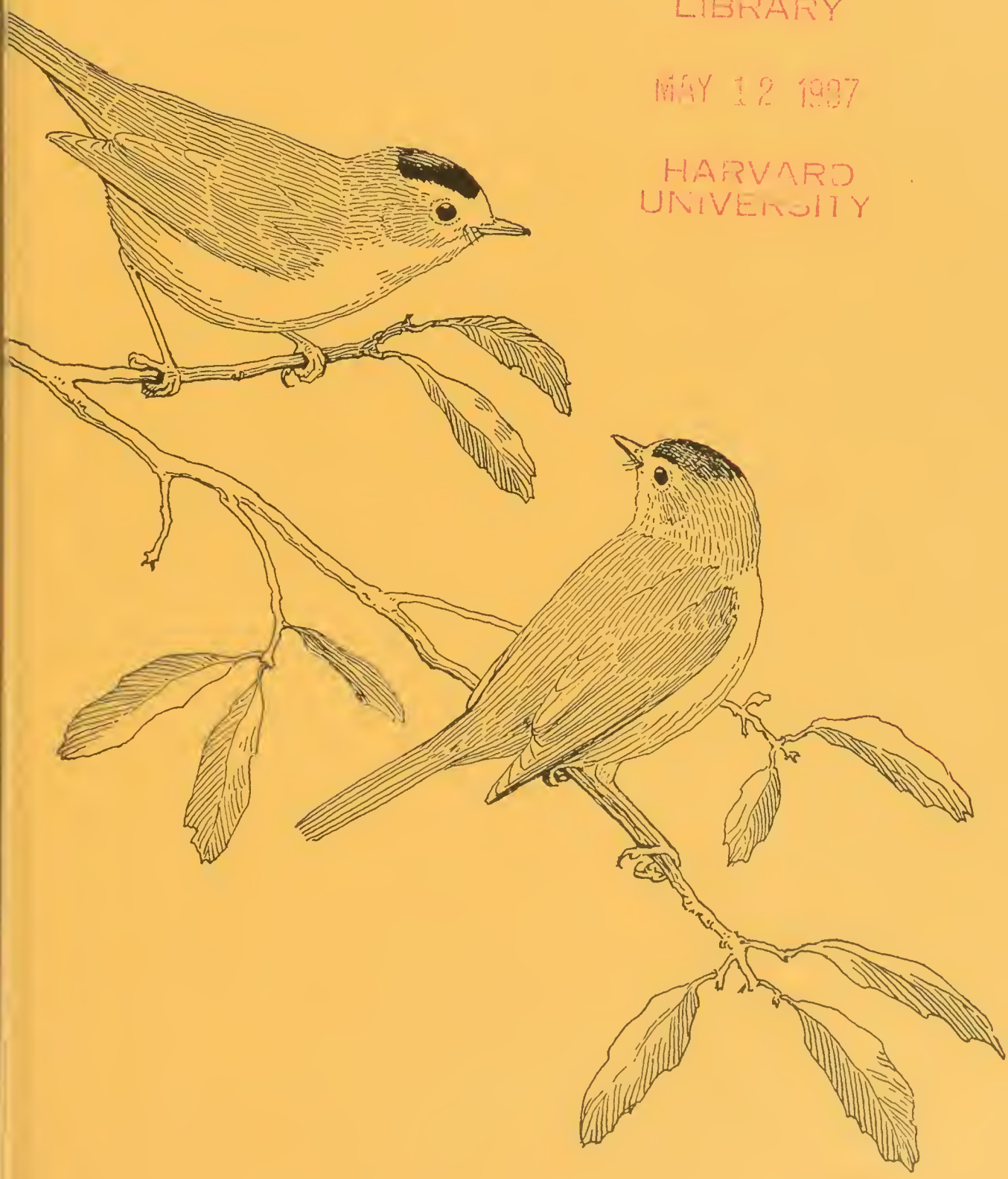

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FOUNDED DECEMBER 3, 1888

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The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 195 periodicals as gifts and in exchange for *The Wilson Bulletin*. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan 48109. Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically. A list of currently received periodicals was published in the December 1978 issue.

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All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109. Known office of publication: OSNA, Department of Zoology, 1735 Neil Avenue, Ohio State University, Columbus, OH 43210. POSTMASTER: Send address change to *The Wilson Bulletin*, OSNA, P.O. Box 21618, Columbus, OH 43221.

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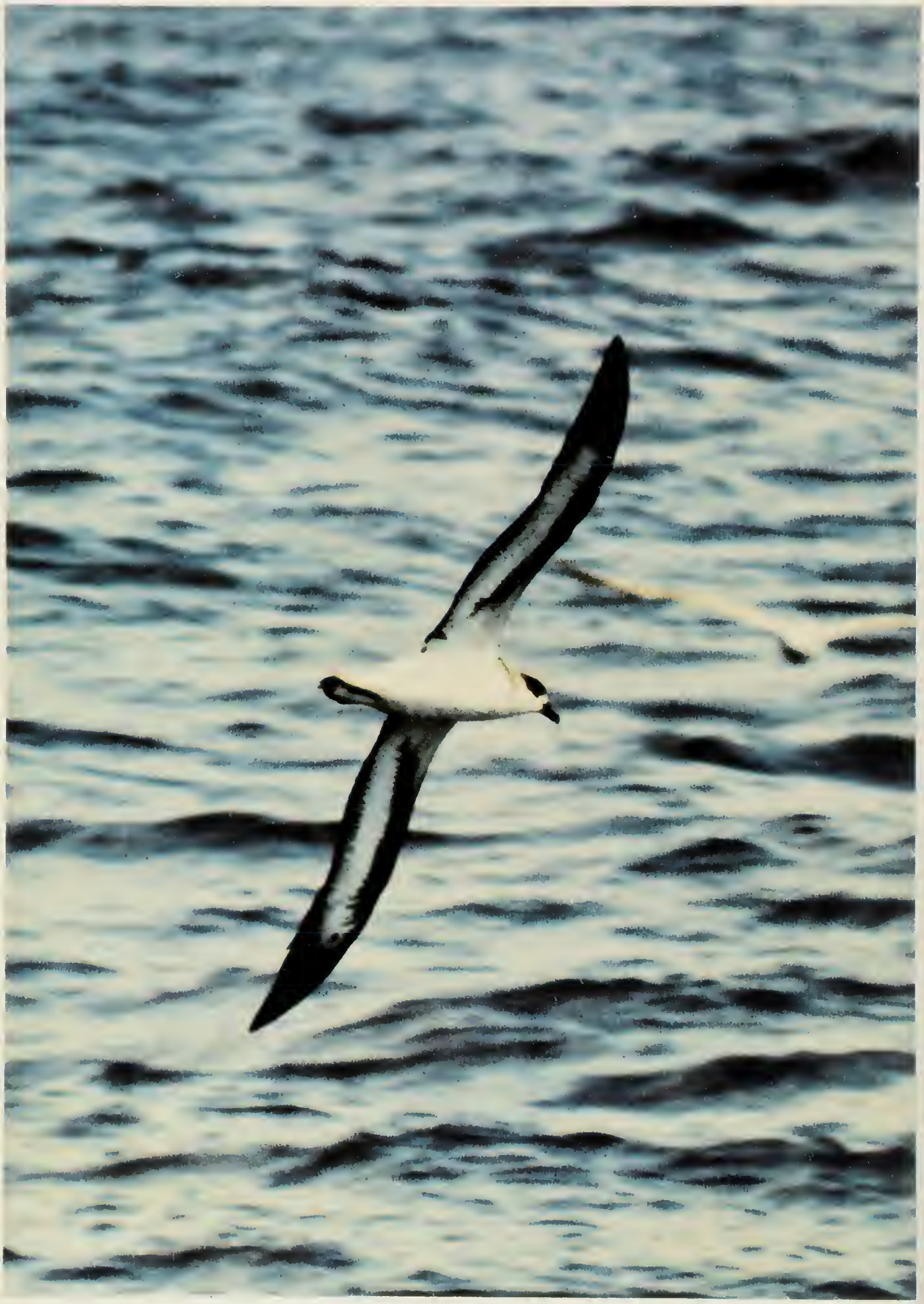

Black-capped Petrel *(Pterodroma hasitata)*
in the Gulf Stream off Georgia, April 1984.
Photo by J. C. Haney.

THE WILSON BULLETIN

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Wilson Bull., 99(2), 1987, pp. 153–168

ASPECTS OF THE PELAGIC ECOLOGY AND BEHAVIOR OF THE BLACK-CAPPED PETREL (*PTERODROMA HASITATA*)

J. CHRISTOPHER HANEY[1]

ABSTRACT.—Recent seabird surveys off the coast of the southeastern United States indicate that petrel distribution is most influenced by the Gulf Stream and other warm water masses between 10° and 40°N latitude. Gulf Stream meandering and topographically induced current deflection affected petrel distribution at meso-scales (100–1000 km) between Florida and North Carolina. Locally (10–100 km), petrel distribution was influenced by the presence of upwelling associated with Gulf Stream eddies and the mesas, ridges, and hills on the Blake Plateau. Sea surface temperature and depth alone did not adequately characterize the petrel's marine habitat.

Petrels used three modes of flight, and their flight behavior was strongly influenced by wind speed. During the day they were most active in early morning and late afternoon, when all observed feeding took place. Petrels also may have fed crepuscularly and at night. Most feeding occurred in mixed species flocks at either natural food sources (fish and invertebrate swarms) or on chum at fishing vessels. Petrels did not rely exclusively on olfaction for locating food sources. They fed on cephalopods, small fish, and fauna associated with the macro-alga *Sargassum*. *Received 7 Jan. 1986, accepted 14 Apr. 1986.*

The Black-capped Petrel (*Pterodroma hasitata*), once thought to be extinct (Bent 1922), is the only gadfly petrel known to breed in the West Indies. The species has been observed infrequently during the last century. Only since the 1970s (Lee 1977, Lee and Booth 1979) have Black-capped Petrels been considered regular visitors to some offshore zones of the southeastern United States, apparently the species' primary nonbreeding range (Clapp et al. 1982). The sizes, locations, and chronologies of petrel breeding colonies remain little known (Wingate 1964, van Halewijn and Norton 1984). The Gulf Stream current is thought to be a principal factor

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influencing the marine distribution of this species (Clapp et al. 1982, Lee 1984). Here I examine the pelagic ecology and behavior of petrels observed off the coast of the southeastern United States in relation to Gulf Stream variation. Additional observations of postbreeding phenology, behavior, interspecific feeding associations, and foraging are also given for the species.

STUDY AREA AND METHODS

Observations of Black-capped Petrels were made during 173 days of seabird surveys in the western North Atlantic Ocean from 1982 to 1985. Except for a 14-day cruise from Boothbay Harbor, Maine, to Bermuda and return, all observations were made between 28° and 35°N latitude off the coast of the southeastern United States. The principal differences between the marine environment of this region and other western North Atlantic sectors stem from (1) the proximity of the Gulf Stream to shelf water masses; (2) a wide (80–160 km) and shallow continental shelf uninterrupted by ledges, banks, or submarine canyons; and (3) the absence of a typical continental slope (Atkinson et al. 1983). The Blake Plateau, a topographic anomaly that lies between the continental shelf and slope, extends 100–150 km seaward of the continental shelf before steep bathymetric gradients are encountered. Waters deeper than 1000–2000 m are not found within 150–250 km of the coastline in the study area (southern North Carolina to northern Florida).

My methods for counting seabirds have been described elsewhere (Haney and McGillivary 1985). Counts employed a 300-m band transect and 15-min count interval. This method permitted expressing the abundances of Black-capped Petrels either per surface area censused or per count hour (Table 1).

During 2326 counts I recorded date, latitude and longitude, heading of ship and birds, ship speed, time of day, visibility, sea height, wind speed and direction, depth, and sea surface temperature (SST). Foraging associations and behavior of Black-capped Petrels were recorded while conducting in-transect counts and when ships were on station.

The distribution and abundances of Black-capped Petrels were compared to long-term Gulf Stream current statistics (Olson et al. 1983), or to Gulf Stream System Flow Charts (National Oceanic and Atmospheric Administration, Miami, Florida) that gave synchronous daily summaries of oceanographic conditions within the study area and along the cruise track. Black-capped Petrels were counted and their abundances compared among seven Gulf Stream eddies that differed in age and size. The ages of eddies were determined by examining time series of Gulf Stream System Flow Charts for initial eddy formation. Age approximated elapsed time since onset of upwelling at the eddy. Eddy sizes were computed by measuring their areal coverage or surface area from the charts.

Black-capped Petrels exhibit considerable variation in size, color, and the extent of white on the nape and base of the tail (Harrison 1983, Lee 1984). All white-naped and white-rumped *Pterodroma* were treated as ecologically equivalent in this study. These morphs, however, may represent breeding populations that differ in dispersal, distribution, and breeding chronologies.

DISTRIBUTION AND PHENOLOGY

Black-capped Petrels are confined to tropical and subtropical water masses in the western North Atlantic Ocean between 10° and 40°N latitude (Fig. 1). The species is known to breed only on Hispaniola (Massif de La Selle and Massif de La Hotte in Haiti; Sierra Baoruco in the Dominican

TABLE 1
SUMMARY OF SHIPBOARD COUNT EFFORT OFF THE SOUTHEASTERN UNITED STATES (1982–1985)

	Census hours	Surface area (km²)
Inner shelf	91 (17)[a]	457.5 (18)[c]
Middle shelf	137 (26)	661.5 (27)
Outer shelf	158.5 (30)	669.0 (27)
Gulf Stream	143 (27)	668.4 (28)
Winter	58 (12)[b]	293.6 (12)
Spring	166 (31)	823.2 (33)
Summer	166 (31)	678.8 (27)
Fall	139.5 (26)	680.8 (28)
Total	529.5	2476.4

[a] Inner shelf: 0–20 m depths; middle shelf: 21–40 m; outer shelf: 41–200 m; Gulf Stream: 201–900 m (% of census time by location).
[b] Winter: Dec.–Feb.; spring: Mar.–May; summer: June–Aug.; fall: Sept.–Nov. (% of census time by season).
[c] Surface area (% surface area by location or season).

Republic) and in the Sierra Maestra in Cuba (van Halewijn and Norton 1984; R. van Halewijn, pers. comm.).

At sea, almost all Black-capped Petrels have been seen near breeding colonies or along the Gulf Stream in the South Atlantic Bight (Cape Canaveral, Florida, to North Carolina) (Lee 1977, 1984; Clapp et al. 1982; Haney 1983). Petrels occur in winter and spring north and south of Hispaniola, and near Puerto Rico and the Virgin Islands (Morzer Bruijns 1967a; Norton 1983, 1984). There are also records from the central eastern Caribbean and near the leeward Netherlands Antilles, but apparently no reliable observations from the western North Atlantic Ocean east of the West Indies (Voous 1983; R. van Halewijn, pers. comm.), and no pelagic observations from the Gulf of Mexico (Clapp et al. 1982). An old record of the Black-capped Petrel off Brazil (AOU 1983) is apparently unsubstantiated by details (R. van Halewijn, pers. comm.).

Black-capped Petrels occur at least occasionally north or east of the South Atlantic Bight. Single birds and small groups have been seen off Virginia and Maryland (Rowlett 1977, Harrison 1983) and north to about 40°–45° in the northwest Atlantic off New England and southern Canada (Brown 1973; Lambert 1977, pers. obs.), areas that are directly or indirectly influenced by the Gulf Stream (Fig. 1). Black-capped Petrels may also occur east of the Gulf Stream in the western Sargasso Sea (Nieboer 1966, Morzer Bruijns 1967b), but I saw none during 2 weeks of daily observations in the Sargasso Sea in August 1984. The species is accidental in the northeast Atlantic. A single specimen record (1852) exists for En-

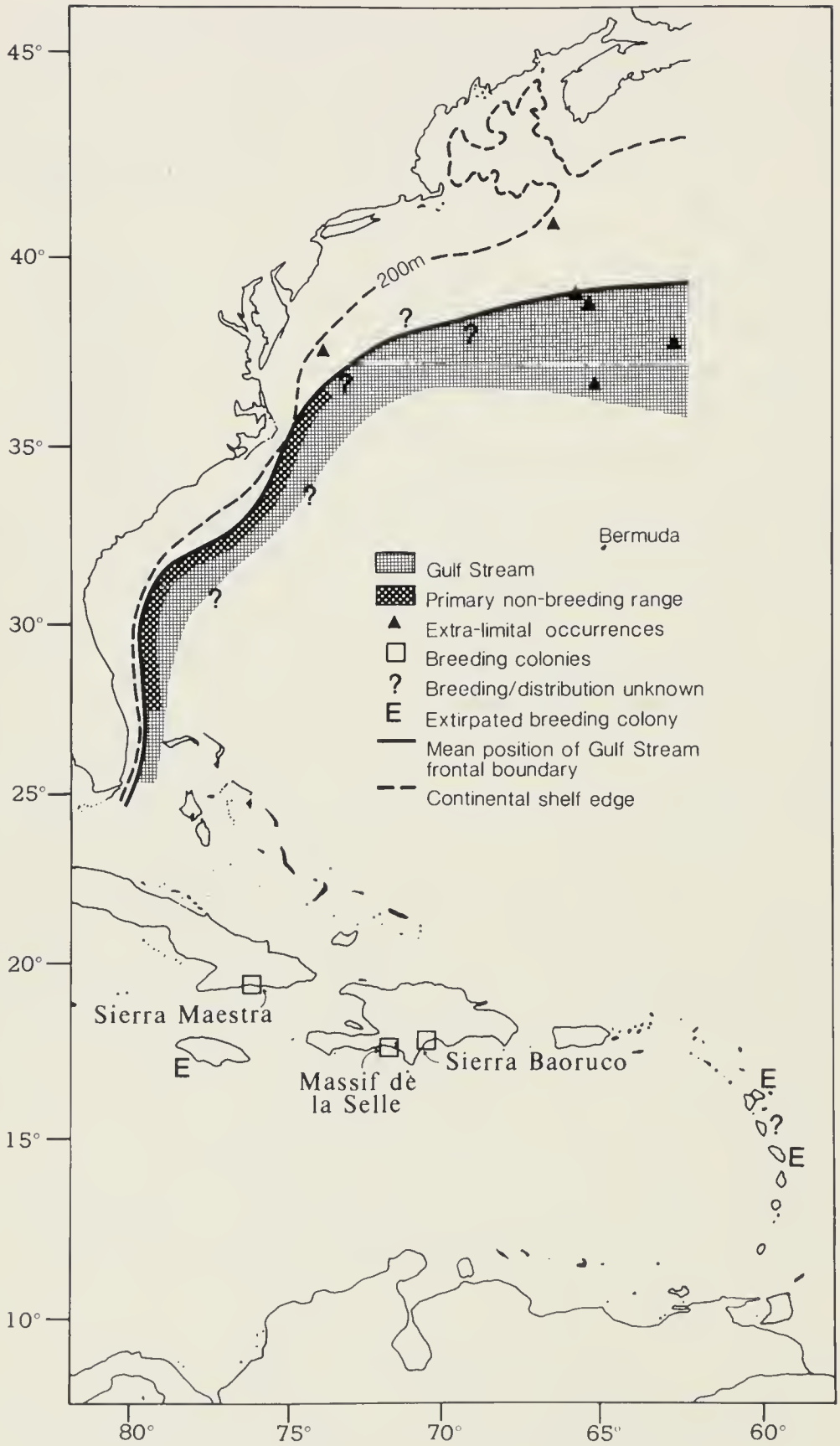

FIG. 1. Breeding colonies and marine distribution of Black-capped Petrels in the western North Atlantic Ocean. Extralimital occurrences north of 36° came from personal observations and literature accounts (Brown 1973, Lambert 1977, Rowlett 1977, 1980).

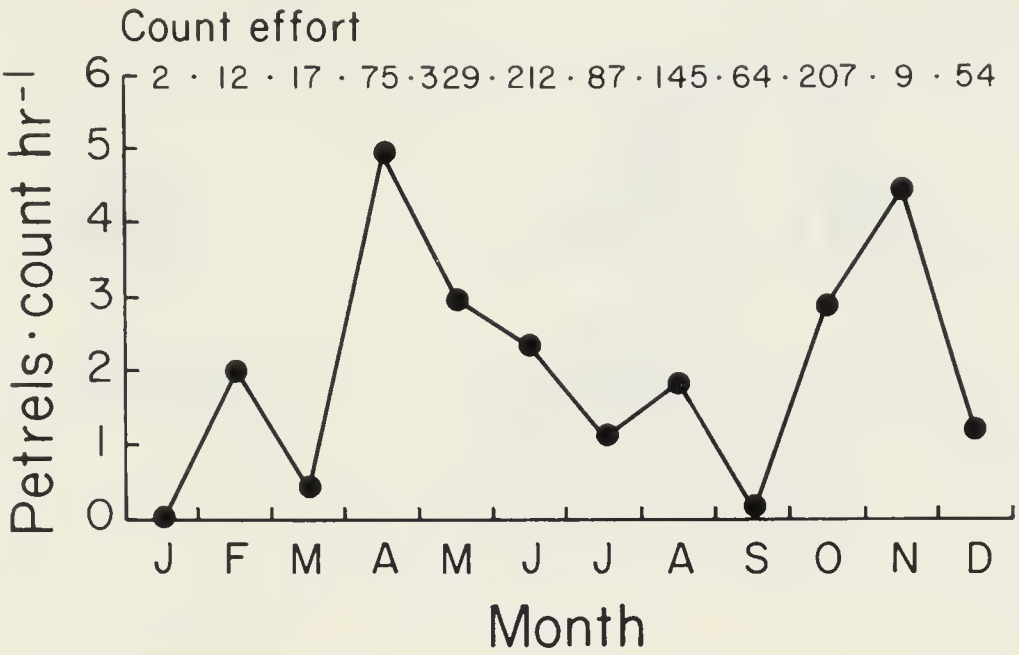

FIG. 2. Seasonal abundance of the Black-capped Petrel off the southeastern United States between 28° and 35°N latitude. Effort refers to number of 15-min counts made during the month on the outer shelf and in the Gulf Stream (Table 1).

gland, and there is a recent sight record from the Rockall Bank (Cramp and Simmons 1977, Bourne 1983).

Black-capped Petrels were observed offshore of South Carolina, Georgia, or Florida each month except January, when, because of inclement weather, very few offshore counts were conducted (Fig. 2). Peak abundances were recorded in spring and fall when the species moves from or to breeding colonies.

MARINE HABITAT

The primary marine habitat of the Black-capped Petrel off North Carolina lies seaward of the continental shelf break (200 m isobath), an area including, but not limited to, the Gulf Stream (Lee 1984). Petrels occurred almost exclusively within the cross-shelf interval of Gulf Stream frontal meandering in the South Atlantic Bight (Fig. 3). Gulf Stream position relative to the shelf changes during 2- to 14-day periods as a consequence of wave-like propagations along the current boundary (Lee and Brooks 1979, Lee et al. 1981, Lee and Atkinson 1983, Olson et al. 1983). Petrel affinities for the Gulf Stream current boundary resulted in changes in the species' distribution with respect to depth and distance offshore. Off Florida, Black-capped Petrels occurred over shallower depths and closer to land than farther north off Georgia and South Carolina. Broader cross-shelf distributions of Black-capped Petrels at higher latitudes also cor-

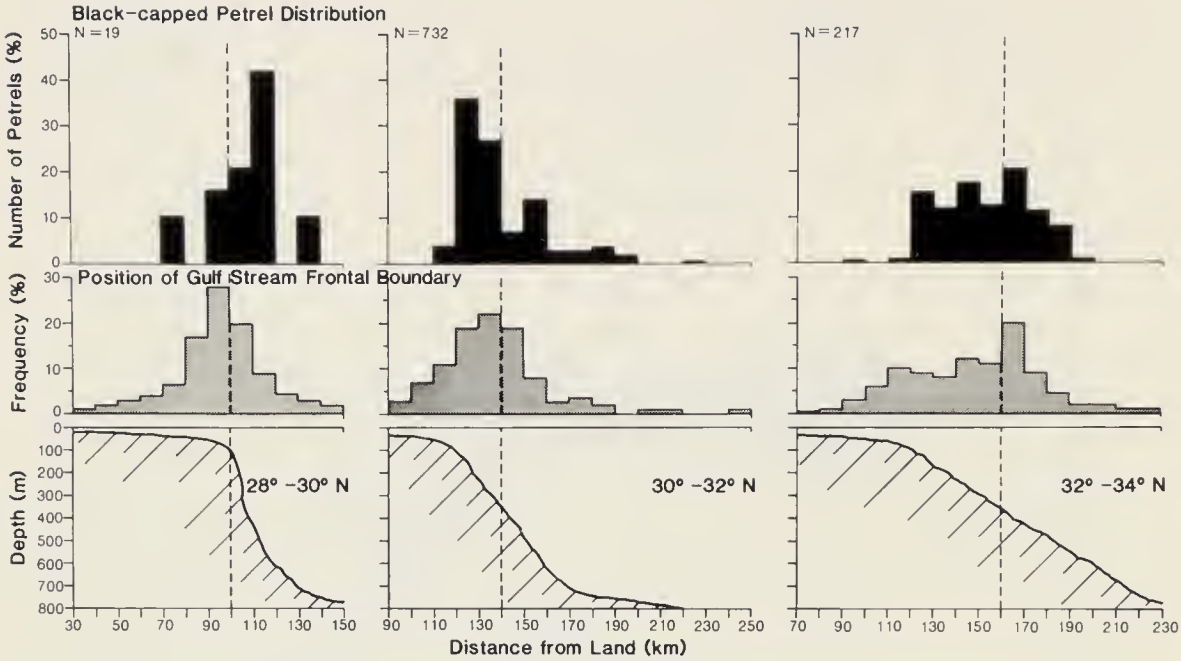

FIG. 3. Cross-shelf distribution of the Black-capped Petrel and its relationship to depth, distance from land, and the position of the western Gulf Stream frontal boundary at three intervals of latitude off the southeastern United States. Black-capped Petrel abundances were converted to frequency histograms (10 km interval) of the cross-shelf locations of individual birds (N refers to sample size). The frequency histograms of Gulf Stream frontal position are based on long-term satellite observations (Olson et al. 1983). The vertical dashed lines indicate mean frontal position.

responded to this increase in the cross-shelf range of frontal meandering (Fig. 3).

East of the western Gulf Stream frontal boundary, Black-capped Petrels were observed only over seamounts, submarine ridges, and mesas on the Blake Plateau. Small numbers of the petrels were seen feeding over and downstream of the Stetson Mesa (30°30′N, 79°30′W) and Hoyt Hills (32°00′N, 78°30′W). Petrels at these locations were primarily observed in or near internal wave crests resulting from topographic turbulence created by the current over steep undersea ridges and peaks.

One hundred to 1000-km scale changes in petrel abundance were correlated with increases in the amplitude of Gulf Stream meandering at higher latitudes (Fig. 4). Unstable meanders induce upwelling (Lee et al. 1981) and cause local increases in the biomasses of marine organisms in the South Atlantic Bight (Yoder et al. 1981, Atkinson and Targett 1983, Paffenhofer et al. 1984, Deibel 1985). Significantly, Black-capped Petrels were most abundant off northern Georgia and southern South Carolina (Fig. 4) where upwelling is most frequent, persistent, and extensive (Brooks and Bane 1978, Legeckis 1979, Bane 1983). Food biomasses may also be higher in this region because of downstream transport and accumulation

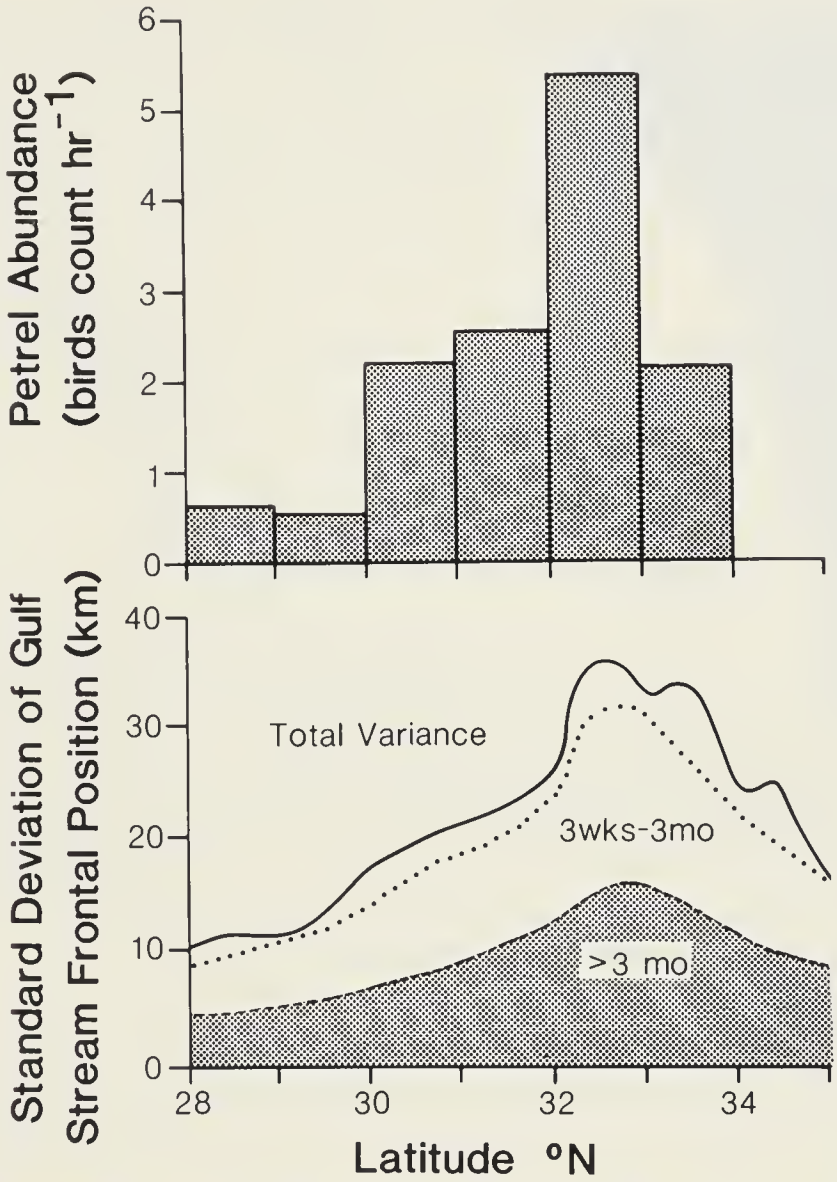

FIG. 4. Relative abundances of Black-capped Petrels at different latitudes off the southeastern United States. Changes in amplitude of Gulf Stream meandering are also shown as a function of latitude (Olson et al. 1983). A breakdown of meander variation at different time scales is included.

of marine organisms from upstream upwelling sites (cf. Yoder et al. 1981, Haney 1986a).

At shorter time scales (days) and at smaller spatial scales (10–100 km), Black-capped Petrels were unequally distributed along the Gulf Stream frontal boundary. Peak abundances occurred at temporary and kinetic frontal eddies (Fig. 5), upwelling features with elevated productivity (Yoder et al. 1981). Petrels were more abundant in the immediate frontal region at eddies (e.g., at the 28° and 29° isotherms) (Fig. 5), and in the resident Gulf Stream water itself (Haney 1986b). A few Black-capped

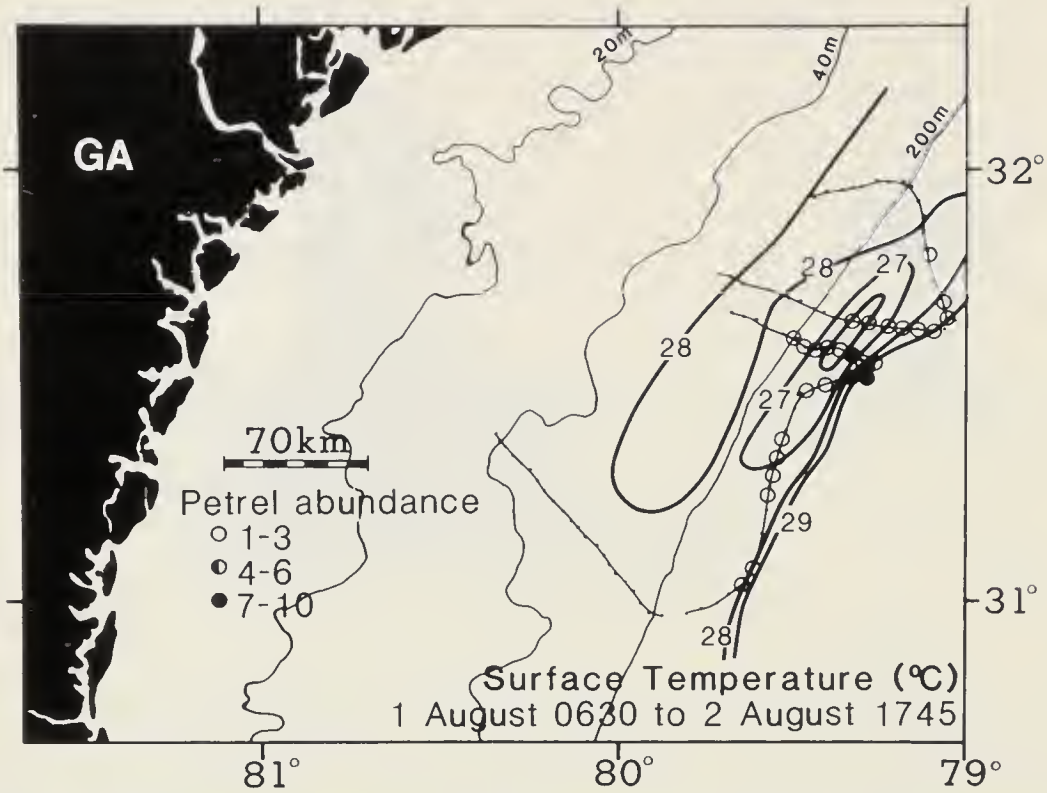

FIG. 5. Distribution and abundance of Black-capped Petrels at a Gulf Stream frontal eddy off the Georgia coast. Gulf Stream waters are those enclosed by the 28° isotherm. Cooler upwelled waters (25–28°C) are surrounded on three sides by warm filament and resident Gulf Stream water. Shelf waters are east of the 28° isotherm and 200-m isobath. Dotted line indicates ship cruise track during daylight hours.

Petrels, however, were occasionally observed in the adjacent upwelled eddy cold-core between the Gulf Stream and shelf waters (see also Lee 1984).

Peak petrel abundances occurred in the older and smaller eddies although no statistically significant correlations (r_s) were detected ($P > 0.10$). As upwelling intensity and the responses of marine organisms to upwelling vary among eddies (Yoder et al. 1983), petrels may have been differentially attracted to eddies that had different prey abundances or species composition, but the exact mechanisms and trophic pathways for the attraction are unknown.

SST and depth did not characterize the Black-capped Petrel's marine habitat over large geographic areas and long time spans. In the South Atlantic Bight, petrels were always observed in the relatively warmer offshore waters at or near the Gulf Stream; however, the absolute sea surface temperatures where petrels were observed varied extensively (20.5°–29.0°C), in part because of seasonal and latitudinal changes in the Gulf Stream (Atkinson et al. 1983). Conversely, Black-capped Petrels did not

occur during summer in shelf waters where SSTs may equal or exceed those in the Gulf Stream (Atkinson et al. 1983, pers. obs.). The influence of depth or bathymetry on petrel distribution was indirect, and was primarily exerted through steering effects of bottom topography on the position of the western frontal boundary of the Gulf Stream (cf. Brooks and Bane 1978, Legeckis 1979, Bane 1983) (Figs. 3, 4).

BEHAVIOR

Petrels usually flew in rapid "roller coaster" flight on bowed and angled wings that produced a distinctive bounding or rising and falling progression (Harrison 1983). Occasionally, they rose to 20–25 m above the sea at the peaks of the arcs. The extent of wing-flapping in this flight mode was inversely related to wind speed. At wind speeds ≤ about 6 knots, petrels used a very slow and labored flight with many deep, rapid wingbeats, particularly when taking off from the ocean surface. Gull-like soaring on horizontal wings from 50–100 m above the ocean surface was observed rarely during moderate wind conditions (6–15 knots).

In higher winds Black-capped Petrels may sometimes spring directly into the air from the water surface (Harrison 1983). In low winds (≤6 knots), they run along the ocean surface for 2–4 m before taking flight (Haney 1983:fig. 2).

Relative petrel abundances increased from Beaufort force 2 to a peak at force 5 (17–21 knots) (Fig. 6). Individuals were not observed in winds ≤4 knots, except when sitting birds were flushed from the ocean surface by ship passage. The majority (72%; N = 19) of all sitting birds observed during transits, as well as 100% (N = 13) of nonfeeding sitting petrels, were recorded at wind velocities ≤4 knots. Unless petrels are more difficult to detect under conditions of low wind velocity when sitting on the ocean surface, these data suggest that petrels are dependent upon higher wind velocities for foraging and dispersal.

Black-capped Petrels were active during all daylight hours (Fig. 7) with an apparent peak in activity from 07:00–09:00 h and a less pronounced peak from 17:00–19:00 h. Petrels were seen flying in the ship's high-beam search lights at night, although no feeding was observed during these limited observations. All 8 natural (Table 2) feeding aggregations occurred before 09:00 h or after 15:00 h. All 6 chum-feeding aggregations occurred after 15:00 h. *Pterodroma* petrels exploit diel vertically-migrating, mesopelagic nekton (Imber 1985), which selects for crepuscular or nocturnal feeding.

Although petrels were generally silent, individuals at chum slicks occasionally uttered a bleating or "croaking" note, *waaahh* or *aaa-aw,* when feeding (cf. Wingate 1964, Imber 1985).

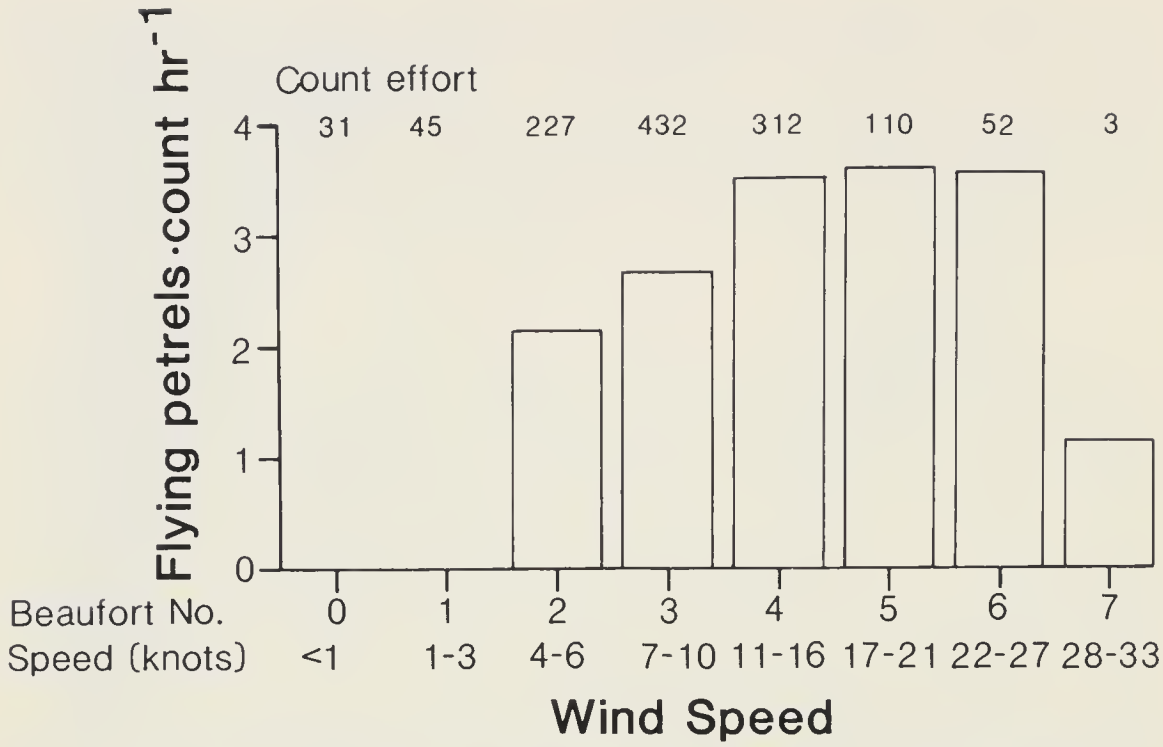

FIG. 6. Relative abundance of initially-flying (see text) Black-capped Petrels as a function of wind speed. Effort refers to the number of 15-min counts made at a particular interval of wind velocity on the outer shelf and in the Gulf Stream.

FORAGING AND FEEDING

The majority (96%) of petrel feeding bouts (N = 25) occurred in flocks, 88% of which included other species. Petrels fed with 12 other species ($\bar{x}$ = 4.3 species/flock; range = 2–8) at baitfish or invertebrate swarms; most frequently with Cory's Shearwaters (*Calonectris diomedea*), Greater Shearwaters (*Puffinus gravis*), Audubon's Shearwaters (*P. lherminieri*), and Pomarine Jaegers (*Stercorarius pomarinus*) in summer, and with Herring Gulls (*Larus argentatus*) and Black-legged Kittiwakes (*Rissa tridactyla*) during winter. Petrels fed with 10 seabird species ($\bar{x}$ = 3.8 species/flock; range = 3–6) at chum slicks, including Greater Shearwaters, Wilson's Storm-Petrels (*Oceanites oceanicus*), and Pomarine Jaegers in summer and Herring and Laughing gulls (*L. atricilla*) in winter. Other less common feeding associates included South Polar Skua (*Catharacta maccormicki*) and Common (*Sterna hirundo*), Bridled (*S. anaethetus*), and Sooty terns (*S. fuscata*). Both Parasitic (*Sterecorarius parasiticus*) and Pomarine jaegers attempted to parasitize nonflying feeding petrels.

My observations of Black-capped Petrels feeding at chum are the first reports for this species (cf. Lee 1979, pers. comm.). During this study petrels frequently flew in to inspect fresh waste fish and fish and chicken entrails near fishing boats. Petrels settled on the water and consumed the

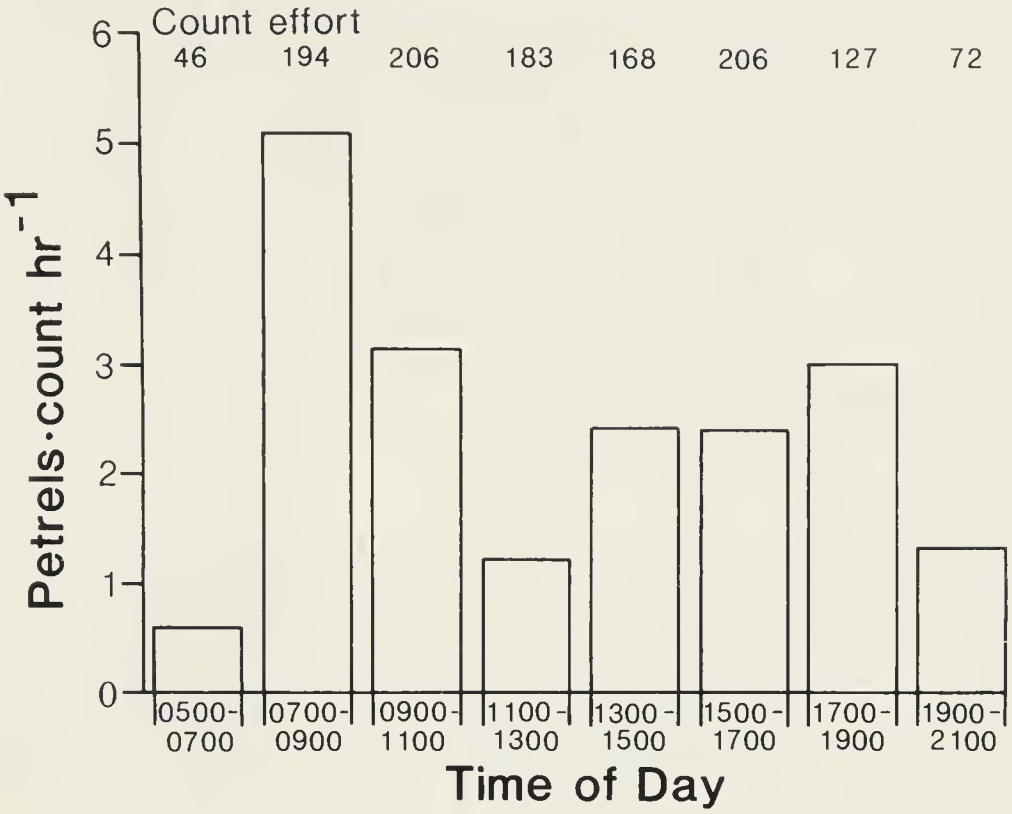

FIG. 7. Diel activity patterns of Black-capped Petrels. The numbers of flying birds per time interval are illustrated. Effort refers to the number of 15-min counts made within a particular time interval on the outer shelf and in the Gulf Stream.

chum, occasionally flying off with large pieces, or attempting to steal the food items from other petrels. On 13 April 1984, 65 petrels fed on fish entrails, with 5 to 10 individuals on the ocean surface continuously. As with several other Procellariiformes (Guzman and Myres 1983), Black-capped Petrels may scavenge discarded waste only when natural foods are not abundant or reliable, such as when large numbers of migrating individuals are locally concentrated.

Black-capped Petrels do not rely exclusively on olfaction for locating food sources as do certain procellariiform birds that are selectively attracted to food-related odors from downwind (Hutchinson et al. 1984). Petrels frequently flew in to inspect seabird individuals or flocks exhibiting foraging behavior from upwind, or from all compass directions.

Petrels used at least 3 foraging postures when feeding: (1) sitting on the ocean surface with wings outstretched and sharply angled backward; (2) aerial dipping and pattering (Ashmole 1971), with their feet extended and touching the ocean surface but still remaining airborne; and (3) less commonly sitting on the ocean surface with folded wings and the head and neck submerged underwater. The latter appeared to be similar to the foraging behavior of the Audubon's Shearwater (Haney 1986c).

TABLE 2

PERCENTAGE OF BLACK-CAPPED PETRELS IN MIXED-SPECIES SEABIRD FEEDING FLOCKS

Food source	Number of petrels		% petrels	
	Mean ± SD	Range (N)	Mean	Range
Natural[a]	5.8 ± 4.4	1–12 (12)	27	1–92
Chum[b]	12.6 ± 18.6	3–65 (10)	47	15–97
Total	8.9 ± 13.1	1–65 (22)	36	1–97

[a] Shoaling baitfish or unidentified invertebrate swarms.
[b] Fish entrails, whole small fish, chicken entrails, and fat.

Petrels spent very little time on the ocean surface. On 5 May 1983, P. W. Stangel (pers. comm.) observed aerial "flushing" and chasing of flying fish by two Black-capped Petrels but did not observe successful capture. On one occasion a petrel was seen diving 3–4 m from the air to, but not beneath, the ocean surface at an angle of 45–60°. This behavior resembled "belly flop" diving or surface plunging by gulls (Ashmole 1971). Petrels were not seen diving beneath the ocean surface.

Petrels fed alone and with other seabird species over schools of baitfish driven to the ocean surface by large predatory fish (e.g., bonito, blue-fin tuna, and Spanish mackerel). They also fed near patches of *Sargassum* where seabird food items may be abundant (Haney 1986c).

Little information is available on the diet of Black-capped Petrels (Clapp et al. 1982). Stomach contents of 3 petrels collected off Georgia (UGAMNH 5243, 5344, 5351) included squid beaks, disarticulated fish bones, fish lenses, whole squid ($\bar{x}$ length = 47.5 mm, range 25–70 mm, N = 4), and one planehead filefish (*Monocanthus hispidus*; length = 40 mm). Other gut contents included very small pieces of petroleum residue, small feathers, paper, and *Sargassum* algal blades. The presence of the algal plant material in all 3 specimens, apparently ingested incidently, and the consumption of *M. hispidus,* suggest that this species forages on *Sargassum*-associated fauna (see Haney 1986c).

DISCUSSION

The nonbreeding range of the Black-capped Petrel is centered in the South Atlantic Bight between North Carolina and Florida. Petrel records off Florida originate from the Cape Canaveral region northward (Clapp et al. 1982). It thus seems likely that Black-capped Petrels migrate from West Indies breeding colonies north and east of the Bahamas via the Antilles Current rather than through the Straits of Florida. The seasonal abundance patterns of petrels (Fig. 2) suggest that the species is widely

distributed during the midsummer near the Gulf Stream to 36°, and perhaps farther north to 40°–45°N. Pelagic surveys in the northwest Atlantic (Brown et al. 1975, Rowlett 1980, Powers 1983) have not been extensive on the continental slope and more oceanic marine habitats of this region. Petrels may occur regularly farther north than present records suggest, especially where Gulf Stream meanders and warm core rings occur near the shelf edge (Rowlett 1980; Haney, unpubl. data).

Black-capped Petrels present off the southeastern United States during the winter breeding season may not yet be reproductively mature, or they may be nonbreeding adults that fail to return to the West Indies. Breeding *Pterodroma* may range up to a few thousand kilometers from nesting sites (Warham et al. 1977), and Black-capped Petrels could disperse to the southeastern United States between incubation shifts (Clapp et al. 1982). Another possibility is that breeding cycles of Black-capped Petrel populations among or within islands are not synchronous such that part of the population breeds in winter while part of the population breeds at another time of the year.

Productivity in the surface waters of the Gulf Stream is very low (Yoder et al. 1983). Few seabirds occur in the Gulf Stream except near the current boundary and where current-generated turbulence at seamounts on the Blake Plateau creates upwelling. The Black-capped Petrel is the only seabird present in the Gulf Stream all year. The behavioral and structural adaptations of gadfly petrels have enabled effective exploitation of ocean niches where prey are widely dispersed (Imber 1985). Their low wing loadings allow efficient gliding (Warham 1977), but not sustained flapping flight. As a result, the Black-capped Petrel is dependent on wind (Fig. 7) for long-distance foraging and dispersal within this oligotrophic environment.

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COLOR PLATE

The Frontispiece photograph has been made possible by an endowment established by George Miksch Sutton. The photograph is by J. C. Haney.

Wilson Bull., 99(2), 1987, pp. 169–174

KARYOTYPES OF FIVE SPECIES OF *EMPIDONAX* FLYCATCHERS

GERALD F. SHIELDS,[1] JON C. BARLOW,[2,3] AND ROSS D. JAMES[2]

ABSTRACT.—Conventional karyotypic techniques were applied to five species of tyrant flycatchers (*Empidonax*) of the family Tyrannidae in order to determine the extent of chromosome differentiation within the group. The karyotypes of the Alder Flycatcher (*E. alnorum*), the Willow Flycatcher (*E. traillii*), and the Hammond's Flycatcher (*E. hammondii*) appeared identical. The Yellow-bellied Flycatcher (*E. flaviventris*) and the Least Flycatcher (*E. minimus*) possess one and three unique chromosomes, respectively. These data suggest an alternative hypothesis for relationships within the group. *Received 11 Aug. 1986, accepted 9 Dec. 1986.*

Karyotypic comparisons of closely related bird species are uncommon (Shields 1982), yet specific trends in karyotypic evolution have now been identified for a variety of better understood nonavian lineages (see White 1978:45–106). Such comparisons might help to elucidate trends in avian chromosome evolution. Herein, we describe the chromosomes of five species of *Empidonax* flycatchers and discuss the taxonomic relationships within this group.

MATERIALS AND METHODS

All birds in this study were captured in mist nets during the breeding season. Specimens of the Alder Flycatcher (*Empidonax alnorum*) and the Willow Flycatcher (*E. traillii*) were all of known song type or mated to males of known song type. Karyotypes were obtained from primary cultures of kidney cells according to the procedures of Shields (1983). At least 10 chromosome spreads of high quality were analyzed for each species. Chromosomes were karyotyped using conventional photographic and measurement techniques. Skins and partial skeletons of birds collected in Ontario were deposited in the ornithology collection of the Royal Ontario Museum, Toronto, (specimens and identification numbers: *E. flaviventris* male, ROM#126751; *E. traillii,* 2 males, ROM#114105, ROM#114107; female, ROM#114106; *E. alnorum,* 2 males, ROM#114153, ROM#114155; *E. minimus,* 2 males, ROM#114188, ROM#115134.

RESULTS

Our culture procedures routinely produce excellent, well spread complements from which the chromosomes can be tentatively paired (Fig. 1). For the comparative studies we felt justified in homologously pairing the 12 largest chromosomes. These macrochromosomes, which are usually

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FIG. 1. Complete karyotype of the Alder Flycatcher (*E. alnorum*).

greater than 1 μ in length, are shown in Fig. 2 for the five species of flycatchers.

Table 1 lists relative chromosome lengths and arm ratios for all species of this study. Of necessity, we arranged chromosomes in order of decreasing size. The karyotypes of conventionally stained chromosomes of *E. alnorum, E. hammondii,* and *E. traillii* appeared identical, with the exception that the *hammondii* sampled was female and thus had Z and W sex chromosomes. The small metacentric chromosome 11 served as a convenient marker. It must be stressed that this alpha level of analysis (White 1978) is only a first approximation of the variability within this group.

The karyotype of the Yellow-bellied Flycatcher (*E. flaviventris*) differs from those just described in that the arm ratio of its first set of chromosomes is clearly smaller (see Fig. 2 and Table 1).

The karyotype of the Least Flycatcher (*E. minimus*) clearly differs from those of the above described species in that chromosomes one, three, and eight possess a unique morphology. No other chromosomes in these respective size ranges among the other species possess such unique morphologies.

DISCUSSION

Our results do not fully support the conventional taxonomy of the group. The chromosomes suggest that *E. alnorum, E. traillii,* and *E.*

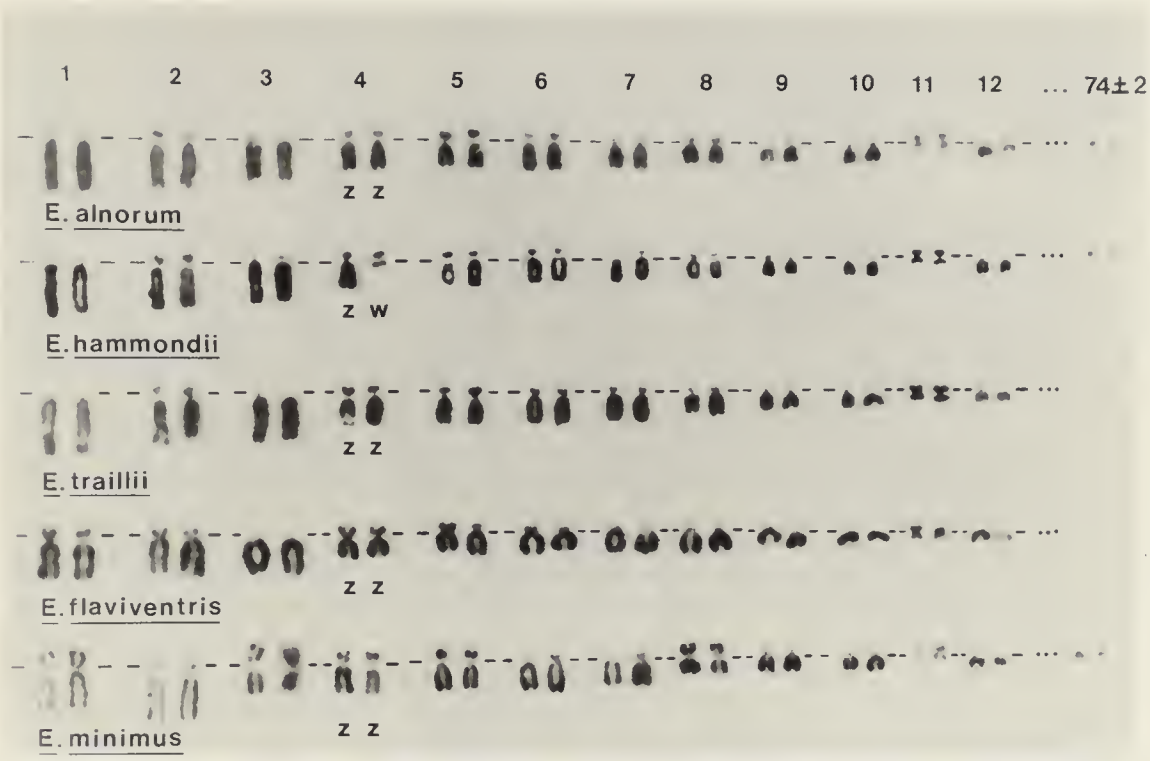

FIG. 2. Karyotypes of the 12 largest chromosomes of five species of flycatchers.

hammondii constitute one natural cluster. *E. flaviventris* differs with regard to the morphology of chromosome one. *E. minimus* appears to form yet a third category.

It is difficult to determine which of the three karyotypes described here is the most primitive. Similarity to some outgroup species would be indicative of common ancestry. Unfortunately, of the nearly 375 other species of tyrant flycatchers recognized worldwide only the Blue-bellied Black Tyrant (*Knipolegus cyanirostris*) has been karyotyped (Lucca and Chamma 1977). Its karyotype is most similar to that of *E. flaviventris,* but chromosome banding studies (Shields 1983) would have to be performed on all species under consideration in order to unequivocally determine the extents of chromosome homology.

Johnson (1980) concluded that *E. traillii* and *E. alnorum* have differentiated the most among several constellations of *Empidonax* flycatchers, but that *E. hammondii* and *E. minimus* are next to them in amount of differentiation. The latter are apparently in an earlier stage of differentiation in his view because they are vocally more similar than *E. traillii* and *E. alnorum,* but they are less similar in morphology and color to each other than they are vocally. Johnson (1980) felt that *E. traillii* and *E. alnorum* are more distinct both vocally and morphologically than *E. hammondii* and *E. minimus.*

TABLE 1

RELATIVE LENGTHS AND ARM RATIOS OF THE TWELVE LARGEST CHROMOSOMES OF FIVE FLYCATCHERS

	Chromosome number											
	1	2	3	4	5	6	7	8	9	10	11	12
Alder Flycatcher												
Relative length	0.138	0.138	0.108	0.101	0.086	0.084	0.079	0.065	0.057	0.050	0.043	0.036
Arm ratio	1:18.0	1:5.3	1:14.0	1:3.6	1:2.0	1:5.5	1:4.5	1:6.5	1:7.0	1:6.0	1:1.0	1:4.0
Willow Flycatcher												
Relative length	0.139	0.133	0.119	0.097	0.097	0.084	0.084	0.069	0.056	0.049	0.042	0.035
Arm ratio	1:19.0	1:5.3	1:16.0	1:3.7	1:3.3	1:5.0	1:5.0	1:6.1	1:8.0	1:6.0	1:1.0	1:4.0
Hammond's Flycatcher												
Relative length	0.147	0.139	0.124	0.101	0.085	0.085	0.078	0.062	0.054	0.046	0.039	0.039
Arm ratio	1:18.0	1:5.1	1:17.0	1:3.3	1:3.9	1:4.5	1:5.1	1:7.0	1:6.0	1:5.0	1:1.0	1:4.0
Yellow-bellied Flycatcher												
Relative length	0.152	0.144	0.110	0.093	0.093	0.085	0.076	0.068	0.051	0.042	0.042	0.042
Arm ratio	1:2.6[a]	1:4.7	1:19.1	1:2.8	1:2.7	1:4.0	1:3.5	1:7.0	1:6.1	1:8.1	1:1.0	1:4.8
Least Flycatcher												
Relative length	0.138	0.131	0.117	0.096	0.096	0.083	0.083	0.076	0.055	0.041	0.041	0.041
Arm ratio	1:1.9[a]	1:5.3	1:4.2[a]	1:2.5	1:2.5	1:5.0	1:3.0	1:1.4[a]	1:7.0	1:5.0	1:1.1	1:3.0

[a] Indicates chromosomes of unique morphology.

The views of Johnson have now been supplemented and modified by electrophoretic data (Zink and Johnson 1984). These data do not support the hypothesis of a close relationship of *E. hammondii* and *E. minimus.* Indeed, *E. minimus* is moderately distinct from all 11 other congeners with which it was compared according to the protein evidence. Thus, the allozyme data are essentially in agreement with the distinctiveness of *E. minimus* as proposed here on the basis of chromosome morphology. The allozyme data, however, do not necessarily support a particularly close relationship of *E. hammondii, E. traillii,* and *E. alnorum,* although the latter two forms are close, as expected.

A solution to the dilemma of nonconvergence between suites of traits using a variety of methodological analyses may be realized when we appreciate that reproductive isolation can be accomplished by various processes, each of which may differ in overall effect and rate. Thus, Templeton (1980) stressed a novel nomenclature for the genetic processes by which reproductive isolation might take place. Such a nomenclature stresses mechanisms which are at the basis of the promotion of reproductive isolation rather than a geographic nomenclature which simply defines whether the incipient species are breeding in sympatry or in allopatry.

Templeton (1980) defines two types of processes that may lead to reproductive isolation but which are markedly different in the way in which the isolation takes place. A *genetic transilience* is defined as reproductive isolation that is accomplished by mutation in a small number of genes but with major effect: Chromosomal rearrangements that become rapidly fixed due to genetic drift are also defined as transiliences. Genetic divergence, as opposed to genetic transilience, occurs when reproductive isolation is accomplished gradually by the effect of mutation on a larger number of genes. Thus, in birds we might expect to see closely related species which are indeed phenotypically similar (e.g., *E. minimus* and *E. hammondii*) but chromosomally distinct. Alternatively, species pairs may be phenotypically divergent (e.g., *E. traillii* and *E. alnorum*), yet they may possess seemingly identical karyotypes.

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WESTERN RAPTOR MANAGEMENT SYMPOSIUM AND WORKSHOP

The Western Raptor Management Symposium and Workshop, coorganized by the National Wildlife Federation and the Idaho Chapter of The Wildlife Society, will be held 26–28 October 1987 in Boise, Idaho. The symposium will feature technical paper sessions on the status of western raptors and their habitats, land-use activities impacting raptors, as well as workshops and a poster session. For more information, contact the National Wildlife Federation, Institute for Wildlife Research, Department 162, 1412 Sixteenth Street, N.W., Washington, D.C. 20036–2266 or call (703) 790–4264.

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HABITAT USE BY BREEDING WILLETS IN THE NORTHERN GREAT PLAINS

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Abstract.—Willets (*Catoptrophorus semipalmatus*) defended multipurpose territories ($\bar{x}$ = 44 ha) including sizeable upland components. Most breeding pairs (90%) and broods (70%), however, were sighted in or near wetlands where they fed. Willets defended areas with greater densities and diversity of wetlands than generally available across the study area. As wetland availability was reduced by drought, Willet density declined. Willet pairs were most often observed in semipermanent wetlands. But based on use vs availability, Willets preferred ephemeral, temporary, seasonal, and alkali wetlands over semipermanent and permanent wetlands. Wetlands used by Willets had significantly greater proportions of more open cover types than those not used. Within used wetlands, Willets made disproportionately frequent use of lightly vegetated sites. Willets made little use of upland habitats, except for nesting. Little selection for upland land-use types was evident, but Willets avoided tilled land. Upland sites used by Willet pairs were dominated by short (<15 cm), native grass cover. Broods used taller grass cover in uplands than did adults. Willet defense of large, multipurpose territories seems related to limited wetland foraging habitats and possible advantages gained by spacing nests to reduce predation. Continued destruction of wetland and prairie habitats likely will reduce Willet populations in the northern Great Plains. Preservation of wetland complexes and management of wetland and upland habitats with grazing, mowing, and prescribed burning treatments are suggested. *Received 4 Apr. 1986, accepted 23 Sept. 1986.*

Two subspecies of Willets (*Catoptrophorus semipalmatus*) breed in North America. An eastern subspecies (*C. s. semipalmatus*) nests along the Atlantic and Gulf coasts from New Brunswick to Mexico and Venezuela, and the western subspecies (*C. s. inornatus*) breeds locally from Oregon to Manitoba and south to Nebraska and Colorado (AOU 1983).

Intensive studies of Willet life history (Vogt 1938; Tomkins 1932, 1955, 1965; Wilcox 1980), social organization (Howe 1982), and nest-site characteristics (Burger and Shisler 1978) have been limited to the Atlantic seaboard. Sordahl (1979) reported on the behavioral and vocal repertoire of Willets breeding in Utah. Higgins et al. (1979) and Weber et al. (1982) presented limited information on nesting and wetland use in the northern prairie region.

The eastern subspecies typically nests in highly productive salt-marsh habitats. Nest densities in these areas are high (Tomkins 1965, Burger and Shisler 1978, Howe 1982), and territories and home ranges are small (Vogt 1938, Howe 1982). In the northern Great Plains, Willet densities

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(Stewart and Kantrud 1972) are much lower than those of the Atlantic coast. Western Willets nest in uplands near brackish or saline wetlands (Bent 1929, Higgins et al. 1979). These prairie habitats likely are less productive and more ephemeral than are salt-marsh communities (cf. Odum 1971:357).

Our objectives were to quantify habitat use and selection by breeding Willets and to compare patterns of habitat use between prairie and salt-marsh populations. Based on the data gathered, we also discuss the possible long-term effects of habitat changes on Willet populations and comment on public land management practices as means for Willet conservation.

STUDY AREA AND METHODS

We gathered data from April through August 1979–1981 on a 1300-km^2 area in Stutsman and Kidder counties in east-central North Dakota. The area is a recently glaciated, irregular plain with numerous shallow wetlands (Bluemle 1977). Approximately 25% of the uplands were comprised of native prairie vegetation, dominated by needlegrasses (*Stipa viridula* and *S. comata*), blue gramma (*Bouteloua gracilis*), and western wheatgrass (*Agropyron smithii*). Most of the native grassland vegetation was grazed, with small percentages cut for hay or left idle. The remainder of our study area consisted of nonnative vegetation, e.g., smooth brome (*Bromus inermis*) and alfalfa (*Medicago sativa*), that was grazed, mowed, or left idle, and annually tilled croplands. Small grains were the most common crop type, but sunflowers, corn, or summer fallow made up a substantial portion of the study area each year (for details see Ryan 1982 and Ryan et al. 1984).

We recognized four basic upland habitat types based on principal land use: (1) pasture—lands currently or recently grazed by livestock, (2) hayfields—lands on which the vegetation was recently mowed, (3) idle grassland—grass-dominated lands showing no evidence of recent grazing or mowing, and (4) tilled—lands on which any recent tillage had occurred. Total availability of upland land-use types was determined once each year by randomly sampling 368 quarter sections along the transect routes.

We measured habitat availability and its use by Willets along 4, approximately 75 km, roadside transects. We drove each transect biweekly throughout the Willet breeding and brood-rearing periods, from late April through July. Transect starting points and times were alternated to compensate for any diurnal patterns of habitat use by Willets. A single transect required from 8 to 14 h to complete.

Along each transect, we mapped and classified all wetland basins within 350 m of the road. Natural wetlands were classified according to Stewart and Kantrud (1971) as ephemeral, temporary, seasonal, semipermanent, and permanent wetlands, which form a continuum of increasing depth and, therefore, probability of retaining water throughout the Willet breeding season. Alkali wetlands vary in size and depth and are highly saline. Many alkali lakes are large and shallow, exhibiting large seasonal fluctuations in the area flooded (Stewart and Kantrud 1971). We recognized manmade stockponds and flooded livestock feedlots as unique wetland habitats. Because Willets confined their use to wetland peripheries, we used shoreline length as a measure of availability of each wetland type. During each transversal of the transects, we remapped wetland boundaries and later recalculated shoreline lengths, resulting in biweekly estimates of the availability of each wetland class.

On transects, we quantified habitat features at the exact site where Willets were observed,

as well as habitat available in the immediate vicinity. For comparison, we also measured habitat characteristics at sites where no Willets were observed. During each transect transversal, we randomly sampled 15 unused wetlands and 15 unused upland sites. Wetlands were chosen by assigning numbers to all wetlands and a sample chosen using a random numbers table. Upland sites sampled were centered at points 100 m toward the transect route from numbered wetlands. Upland areas to be sampled also were chosen using a random numbers table.

Each wetland, used or unused, was classified and assigned to salinity categories based on vegetative characteristics (Stewart and Kantrud 1971). We estimated the relative coverage of 5 height-canopy coverage categories (*sensu* Daubenmire 1959) along shorelines of all used and randomly selected unused wetlands. Coverage was quantified in two zones along the shoreline; a 3-m wide shallow water strip and a 5-m wide dry shore area. The cover categories composed a continuum from open habitat to tall, dense cover, and included open water (shallow water zone) or bare soil (shore zone), short-sparse (<15 cm tall and <75% dense) canopy coverage, moderately-short-sparse (<15 cm, >75% dense, or 15–60 cm, <25% dense) canopy coverage, moderately-tall-dense (15–60 cm, >25% dense) canopy coverage, and tall-dense (>60 cm, >25% dense) canopy coverage.

At used and unused upland sites, land-use type was identified and the percentage cover of 3 vegetation height categories estimated for a 200-m radius circle centered at the spot occupied by the Willet and the randomly chosen point. Height categories were <15 cm, 15–60 cm, and >60 cm. We also recorded vegetation height at the point where the Willet was first seen.

Transect data were supplemented with observations of 16 individually color-banded Willets. Long-handled dipnets or spring-loaded hoopnets were used to capture Willets at nests. Territories were mapped by observing responses to taped Willet calls and from long-term observations of individuals. From 25–>100 observations were used to plot territory boundaries. Wetlands within territories were classified and counted. For comparison, 100 randomly selected areas (10 replications of each of the Willet territories) also were mapped and wetlands recorded. These areas were chosen by dividing the 700-m wide transect routes into parcels to match Willet territory sizes, numbered, and selected using a random numbers table. Habitat use by marked birds was quantified by recording cover-type occupancy every 15 sec during focal animal sample periods.

Differential use of habitat types was evaluated in three ways. Used and unused habitat cover types were compared using multivariate analysis of variance (MANOVA). Within used habitats, use and availability were compared with goodness-of-fit procedures (χ^2) and with a rank analysis procedure developed by Johnson (1980). Johnson's "usage-availability" analysis computes the mean difference of use and availability ranks for each habitat component. Larger negative values indicate greater disproportionate use (preference). Preference ranks for each habitat component are then compared by using a Duncan-Waller multiple comparison test. The result is a ranking of habitat components based on preference, with a significance test of the rankings. Arcsine transformations were made of percentage data used in MANOVA analyses.

RESULTS

The Willets that we observed defended large feeding and nesting territories ($\bar{x}$ = 44.3 ± 8.6 ha [SE], N = 10). Although large upland areas were defended, 90% (322/355) of the breeding Willets and 70% (33/45) of the broods seen during transect surveys were in or immediately adjacent

to wetlands. Feeding was limited, almost exclusively, to shallow water or adjacent shore areas.

Wetland use and selection.—Total wetland shoreline availability and the relative availability of shoreline along different wetland classes changed annually (Table 1). Pond counts in early May, along our transects, totaled 615 wetlands in 1979, 351 in 1980, and 235 in 1981. The change in wetland conditions was paralleled by a decline in the number of Willet pairs observed during transect samples. During the peak of the nesting seasons, counts averaged 8.8 pairs/transect in 1979, 7.8 in 1980, and 5.8 in 1981 (1979 vs 1981, $P < 0.05$, N = 12, Mann-Whitney U statistic, multiple comparison test).

Although breeding Willets were seen most frequently using semipermanent ponds, comparison of use with availability (Johnson 1980) indicated relatively low preference for this wetland type (Table 1). The proportional use by Willets of ephemeral, temporary, seasonal, and alkali wetlands was consistently greater than the availability of those pond types. And each of those pond types was ranked significantly higher in preference than semipermanent wetlands (Table 1). Permanent lakes were ranked as least preferred each year and received substantial use by Willets only in 1981, when alternative wetland habitats were scarce.

Willets defended areas that had greater wetland densities and diversity than were available across the study area as a whole. Territories had a mean of 7.1 ± 2.3 [SE] (range = 1–22, N = 10) wetlands within their boundaries, whereas randomly located, equal-sized areas averaged only 1.5 ± 0.1 (range = 1–5, N = 100; $P < 0.005$, Mann-Whitney U-test). Territories also had more different types of wetlands than randomly located areas (territories: $\bar{x} = 3.0 \pm 0.3$, range = 1–3; random: $\bar{x} = 1.3 \pm 0.7$, range = 1–3; $P < 0.005$, Mann-Whitney U-test). The frequencies of occurrence of temporary, seasonal, and alkali wetlands were significantly higher in territories than in the randomly chosen areas (Table 2).

Along the Atlantic Coast, Willets are associated closely with saline wetlands, and Tomkins (1965) suggested that Willets in South Carolina and Georgia avoided freshwater sites altogether. We found no evidence that Willet use of wetlands was influenced by salinity. Freshwater ephemeral and highly saline alkali wetlands were equally selected (Table 1). The distributions of salinity categories by wetland class (Stewart and Kantrud 1971) for wetlands used by Willets and those unused did not differ (χ^2 goodness-of-fit tests; temporary, $\chi^2 = 1.3$, df = 1, $P > 0.25$; seasonal, $\chi^2 = 1.4$, df = 2, $P > 0.25$; semipermanent, $\chi^2 = 2.0$, df = 3, $P > 0.5$; permanent, $\chi^2 = 2.3$, df = 3, $P > 0.5$).

Different wetland classes varied in shoreline cover composition. Based on data from randomly selected wetlands over 3 years, ephemeral and

TABLE 1

PERCENT AVAILABILITY OF WETLANDS AND PERCENT USE BY BREEDING WILLETS

Wetland class	1979 Use (119)[a]	1979 Availability (1021)[b]	1979 Preference score[c]	1980 Use (120)	1980 Availability (767)	1980 Preference score	1981 Use (83)	1981 Availability (549)	1981 Preference score
Ephemeral	11.8	4.4	−1.3A	3.3	1.2	−1.0A	1.2	0.3	—[d]
Temporary	9.2	6.8	−0.7A	2.5	1.0	−0.9A	1.2	0.3	—
Seasonal	22.7	18.1	−0.6A	12.5	7.5	−0.7A	7.2	3.9	−0.6A
Semipermanent	36.1	42.0	+0.7BC	40.8	49.1	+1.2B	38.6	42.9	+0.4B
Permanent	7.6	17.2	+1.8C	15.0	29.3	+1.5B	34.9	39.8	+0.4B
Alkali	12.6	9.5	−0.1AB	23.3	10.4	−0.2A	12.1	10.8	−0.3A
Feedlot	0.0	1.5	—	2.5	0.7	—	3.6	0.7	—
Stockpond	0.0	0.5	—	0.0	0.8	—	1.2	1.2	—

[a] Number of Willet pairs observed.
[b] Total km of shoreline sampled.
[c] Use vs availability analysis (Johnson 1980). Scores with the same letter are not significantly different ($P > 0.05$).
[d] Insufficient data to include in use vs availability analysis.

TABLE 2
FREQUENCY OF OCCURRENCE OF WETLAND TYPES IN WILLET TERRITORIES AND RANDOMLY SELECTED AREAS OF EQUIVALENT SIZE

Wetland class	Territories (N = 10)	Random[a] (N = 100)	P^b
Ephemeral	0.1	0.05	>0.05
Temporary	0.6	0.10	<0.005
Seasonal	0.6	0.23	<0.01
Semipermanent	0.8	0.49	>0.05
Permanent	0.5	0.27	>0.05
Alkali	0.3	0.08	<0.05
Feedlot	0.0	0.06	>0.05
Stockpond	0.0	0.02	>0.05

[a] See methods section.
[b] χ^2 contingency test.

alkali wetlands were characterized by low coverage of tall-dense vegetation (6.0 and 5.5%, respectively) and substantial amounts of short-sparse to moderately-tall-dense cover types and open water. Tall-dense vegetation was intermediate in coverage in temporary (23.6%) and seasonal (24.4%) wetlands and dominated the shorelines of semipermanent (53.6%) and permanent (50.6%) wetlands (see Ryan 1982, Ryan et al. 1984).

Wetlands used by Willets differed significantly from unused wetlands in shoreline cover composition (Tables 3 and 4). Changing water levels, related to the drought, resulted in differences in the use and availability of cover types over the 3 years. But in each year, used wetlands had greater proportions of more open cover types than did unused wetlands. Large proportions of tall-dense and moderately-tall-dense cover typified unused wetlands.

Within used wetlands, we frequently saw Willets using all cover conditions except the tall-dense type (Table 3). In the shallow water zone, Willets used short-sparse cover in higher frequencies than its availability each year. The moderately-short-sparse and open water cover types were used disproportionately more in one of the three years. We observed Willets less frequently in the shore zone, and use of cover types there differed from availability to a lesser degree. Moderately-short-sparse, short-sparse, and bare soil cover types received use in excess of availability.

We tested for detection bias in dense cover types (i.e., that fewer Willets than expected were seen in moderately-tall-dense and tall-dense cover) by comparing the transect data with the time Willets spent in different cover types during time budget observations (N = 13.1 h, 19 individuals). Unexpectedly, we saw Willets in the 2 denser cover types more often

TABLE 3

MEAN PERCENT AVAILABILITY OF SHORELINE COVER TYPES AND PERCENT USE BY BREEDING PAIRS OF WILLETS

	Shallow water zone			Shore zone		
		Availability			Availability	
Cover types	Use	Used wetlands	Unused wetlands	Use	Used wetlands	Unused wetlands
1979	(93)[a]	(145)[b]	(189)[b]	(35)	(144)	(189)
Open water or bare soil	9.7	25.6	6.7	11.4	8.8	3.4
Short-sparse	39.8	14.8	5.2	5.7	1.8	1.3
Moderately-short-sparse	17.2	7.9	3.2	34.2	34.0	12.3
Moderately-tall-dense	30.1	40.5	59.9	48.6	48.6	72.9
Tall-dense	3.2	11.3	25.1	0.0	6.9	10.0
	$P < 0.001$[c]	$P = 0.0001$[d]		$P > 0.25$	$P = 0.0001$	
1980	(107)	(159)	(270)	(26)	(160)	(270)
Open water or bare soil	37.4	42.5	20.1	42.3	23.0	9.9
Short-sparse	45.8	25.4	13.3	23.1	19.1	7.1
Moderately-short-sparse	3.7	5.9	3.5	19.2	17.9	16.8
Moderately-tall-dense	13.1	15.5	26.0	15.4	27.8	38.4
Tall-dense	0.0	10.7	37.4	0.0	11.9	27.2
	$P < 0.001$	$P = 0.0001$		$P < 0.05$	$P = 0.0001$	
1981	(74)	(118)	(272)	(40)	(118)	(272)
Open water or bare soil	64.8	50.9	28.5	55.0	35.3	14.1
Short-sparse	23.0	14.7	6.8	0.0	6.8	2.5
Moderately-short-sparse	4.1	3.2	1.5	17.5	8.4	7.1
Moderately-tall-dense	8.1	11.4	15.8	27.5	17.0	21.9
Tall-dense	0.0	20.0	47.6	0.0	32.9	54.3
	$P < 0.005$	$P = 0.0001$		$P < 0.01$	$P = 0.0001$	

[a] Number of Willet pairs observed.
[b] Number of wetlands sampled.
[c] Probability of greater χ^2 value; Goodness-of-fit test, use vs availability within used wetlands.
[d] Probability of greater F-statistic; MANOVA, comparison of availability in used and unused wetlands.

(14% of the time) during transects than during focal animal observations (3%). A hypothesis of fewer Willet sightings in dense cover during transect observations was rejected ($\chi^2 = 137.1$, df = 1, $P < 0.005$, one-tailed goodness-of-fit test).

Sighting Willet broods was difficult, and we obtained few data. Sixty percent of the broods using wetlands were at semipermanent ponds. Seasonal ponds were the most preferred, based on use-availability comparisons (Table 5). The data suggest that ephemeral and temporary ponds were moderately available but were not used. Availability was not predictable, however; ephemeral and temporary ponds held water only briefly after infrequent rains.

TABLE 4
SHORELINE COVER-TYPE PREFERENCES OF WILLET BREEDING PAIRS, 1979–1981 COMBINED

Cover type	Preference score[a]
Shallow water zone	
Short-sparse	−1.5A
Moderately-short-sparse	−0.9B
Moderately-tall-dense	+0.3C
Open water	+0.4C
Tall-dense	+1.8D
Shore zone	
Moderately-short-sparse	−1.0A
Short-sparse	−0.7A
Bare soil	−0.1AB
Moderately-tall-dense	+0.6BC
Tall-dense	+1.1C

[a] Use vs availability analysis (Johnson 1980). Scores with the same letter are not significantly different ($P > 0.05$).

The shoreline cover composition of wetlands at which we sighted Willet broods differed significantly from that of unused wetlands (Table 6). Used wetlands had greater proportions of short-sparse to moderately-tall-dense cover than unused wetlands. Based on our limited sightings, we detected no differential use of cover types within used wetlands.

Upland use and selection.—Despite defending large upland areas, Willets made little use of these habitats except for nesting. The greatest use of uplands for feeding occurred in 1981 when wetland availability was at a minimum. Even with our small sample size, differential use of upland land-use types was evident (Table 7). More than 60% of the breeding pairs and broods were seen in pasture habitats, and idle grasslands also received disproportionately frequent use. Willets, however, seemed to avoid tilled land. Willets selected sites dominated by native vegetation over those comprised of introduced species (tilled areas excluded; $\chi^2 = 16.9$, df = 1, N = 25, $P < 0.005$). Of the 18 nests we located, 15 were in native vegetation. Seven nests were in hayfields, 6 in pastures, and 5 in idle grasslands.

Upland habitats used by Willet breeding pairs differed significantly in cover height composition from randomly sampled unused sites (Table 8). Short vegetation predominated within 200 m of sites where we observed Willet pairs. The distribution of vegetation heights at the exact sites where we saw Willets did not differ from that of the immediately surrounding area (Table 8).

Short, sparse cover characterized Willet nest sites. Based on 1-m^2 sam-

TABLE 5
PERCENT AVAILABILITY OF WETLANDS AND PERCENT USE BY WILLET BROODS, WITH MEAN PREFERENCE SCORES, 1979–1981 COMBINED

Wetland	Use	Availability	Preference score[c]
	(32)[a]	(1174)[b]	
Ephemeral	0.0	2.1	—[d]
Temporary	0.0	3.2	—
Seasonal	18.8	12.9	−1.1A
Semipermanent	59.4	45.3	+0.4AB
Permanent	12.5	24.2	+0.9B
Alkali	9.3	10.3	−0.2AB
Feedlots	0.0	0.7	—
Stockponds	0.0	1.0	—

[a] Number of Willet broods observed.
[b] Total km of shoreline sampled.
[c] Use vs availability analysis (Johnson 1980). Scores with the same letter are not significantly different ($P > 0.05$).
[d] Insufficient data to include in use vs availability analysis.

ples centered at the nest, mean cover percentages were 14.5% bare soil, 77.7% vegetation <15 cm, 7.8% vegetation 15-60 cm, and 0.7% vegetation >60 cm (N = 15).

We observed that Willet broods used significantly taller vegetation in uplands than did breeding pairs ($\chi^2 = 25.9$, df = 2, $P < 0.005$). This difference may, in part, be a function of the greater availability of taller vegetation during the brood-rearing period. We detected no significant difference between cover height in uplands used by Willet broods and the randomly sampled unused sites (Table 8). There was, however, a trend toward a higher percentage of taller cover at used areas. This possible selection of taller cover is further substantiated by the lack of sightings of broods in vegetation less than 15 cm tall. Tomkins (1955) noted the use of tall cover by Willet broods in salt marshes in Georgia.

DISCUSSION

Along the Atlantic Coast, most Willets have been reported defending separate nesting and feeding sites (Tomkins 1965, Howe 1982); although Vogt (1938) recorded multipurpose territories in New Jersey. In all cases, territories of eastern Willets seem to be substantially smaller than those we studied in North Dakota. Territory sizes have not been specified in Atlantic Coast studies but may be inferred to be on the order of several hundred m^2 at maximum. The smallest territory we mapped was 17.1 ha.

Howe (1982) suggested that Willet defense of multipurpose territories along the Atlantic Coast was related primarily to food resources. For

TABLE 6

MEAN PERCENT AVAILABILITY OF SHORELINE COVER TYPES AND PERCENT USE BY WILLET BROODS, 1979–1981 COMBINED

	Shallow water zone			Shore zone		
		Availability			Availability	
Cover types	Use	Used wetlands	Unused wetlands	Use	Used wetlands	Unused wetlands
	(8)[a]	(25)[b]	(330)[b]	(13)	(28)	(329)
Open water or bare soil	0.0	11.4	16.8	0.0	7.7	8.5
Short-sparse	37.5	11.5	2.5	23.1	7.4	1.7
Moderate-short-sparse	0.0	3.7	1.0	0.0	9.0	4.7
Moderate-tall-dense	27.5	39.2	27.4	69.2	49.7	46.1
Tall-dense	25.0	34.1	52.2	7.7	26.3	38.7
	$P > 0.75$[c]	$P = 0.0001$[d]		$P = 0.25$	$P = 0.03$	

[a] Number of Willet broods observed.
[b] Number of wetlands sampled.
[c] Probability of greater χ^2 value; Goodness-of-fit test, use vs availability within used wetlands.
[d] Probability of greater F-statistic; MANOVA, comparison of availability in used and unused wetlands.

disjunct territories, he postulated that nest defense probably was an anticuckoldry strategem.

On our study area, Willets persistently defended multipurpose territories throughout the nesting season. We observed relatively few aggressive encounters in upland portions of territories, but we saw song-flights (Sordahl 1979) over the approximate territory boundaries throughout the nesting period. We also elicited aggressive responses to taped *pill-will-willet* calls (Sordahl 1979) played anywhere within the territory boundaries anytime prior to hatching. We did not quantify frequency of territorial song-flights throughout the nesting period, but we believe that the frequency declined as hatching approached.

It seems likely that the large size of the prairie territories we studied was a function of both limited wetland foraging habitat and the possible advantage gained by spacing nests to reduce the risk of predation. We do not rule out the contribution of an anticuckoldry selection force in nest area defense.

Willets showed strong and consistent selection for certain wetland conditions. Shallow wetlands, including alkali lakes, characterized by relatively sparse shoreline cover were preferred throughout our study, despite substantial between-year changes in wetland availability and conditions as a result of drought. Within used wetlands, Willets showed preference for lightly vegetated sites. Willet preference for shorter, sparser cover may be related to easier prey capture, higher prey densities, better surveillance for predators, or easier escape flight.

TABLE 7
MEAN PERCENTAGE AVAILABILITY OF UPLAND LAND-USE TYPES AND PERCENTAGE USE BY WILLET BREEDING PAIRS AND BROODS WITH PREFERENCE SCORES FOR 1979–1981 COMBINED

Land use	Use		Availability	Preference score[a]	
	Pairs	Broods		Pairs	Broods
	(33)[b]	(13)[b]	(3)[c]		
Pasture	60.6	61.5	28.2	−0.4A	−0.8A
Idle grassland	12.1	15.3	10.3	−1.4A	−1.3A
Hayfield	15.2	15.3	24.9	0.0AB	−0.3A
Tilled	12.1	7.7	36.8	+1.8B	+2.3B

[a] Use vs availability analysis (Johnson 1980). Scores with the same letter are not significantly different ($P > 0.05$).
[b] Number of pairs or broods observed.
[c] Number of years; 368 quarter sections sampled each year.

Willets defended territories with higher densities and greater diversity of wetlands than generally available across our study area. In a highly variable environment, defense of large areas with a high diversity of possible foraging sites may be a hedge against unpredictable changes. Semipermanent wetlands may play an important role in this regard. Although our analysis suggests low preference by Willets for these wetlands, this may be an artifact of their widespread abundance. During dry years, or late in summer, semipermanent wetlands may provide vital habitat for adults and broods. Ryan et al. (1984) suggested that a similar habitat selection strategy has evolved in Marbled Godwits (*Limosa fedoa*), which exploit the same prairie environment. The possible importance of different components of wetland complexes at different stages of the breeding cycle of waterfowl also has been noted frequently (Patterson 1976, Swanson et al. 1979, Duebbert and Frank 1984, Mulhern et al. 1985).

With the exception of a strong avoidance of tilled areas, Willets showed little selection for upland land-use types. Breeding pairs did select upland areas with substantially greater amounts of short, sparse cover than were available across the study area. Such sites allowed for easy surveillance for predators by adult Willets. The preference shown for native vegetation, which was typically short to moderate in height, may reflect avoidance of introduced grasses and legumes that exhibited tall, dense growth forms. Willets constructed nests in very short, sparse cover.

Howe (1982) suggested that Willet internest distances, territorial behavior, and predator densities were interrelated. In a seemingly predator-free environment, he reported high nest densities, implied a lack of nest area defense, and recorded no antipredator behavior. At a second Willet nesting area with predators, Howe reported greater internest distances,

TABLE 8

MEAN PERCENT AVAILABILITY OF UPLAND VEGETATION HEIGHT CATEGORIES AND PERCENT USE BY WILLET PAIRS AND BROODS, 1979–1981 COMBINED

Vegetation height	Use	Availability	
		Used sites	Unused sites
Pairs	(32)[a]	(32)[b]	(756)[b]
<15 cm	81.3	72.0	46.6
15–60 cm	18.7	26.6	47.7
>60 cm	0.0	1.5	5.6
	$P > 0.25$[c]	$P = 0.003$[d]	
Broods	(13)	(13)	(360)
<15 cm	0.0	15.7	29.6
15–60 cm	84.6	62.3	52.5
>60 cm	15.4	22.0	17.9
	$P > 0.1$	$P = 0.39$	

[a] Number of pairs or broods observed.
[b] Number of upland sites sampled.
[c] Probability of greater χ^2 value; Goodness-of-fit test, use vs availability within used wetlands.
[d] Probability of greater F-statistic; MANOVA, comparison of availability in used and unused wetlands.

low-level nest area defense, and predator mobbing by Willets. In the Prairie Pothole region where we worked, predation on ground nests is frequent (Miller 1971, Duebbert and Kantrud 1974, Kirsch and Higgins 1976, Sargeant et al. 1984). In North Dakota, Willet defense of large upland nesting areas resulted in long internest distances. In our area, nesting Willets did not mob predators, or us, unless the nest was approached to within a few meters. Instead, the incubating adults seemingly relied on their cryptic coloration for concealment in the large blocks of homogeneous upland habitat. That spacing of nests can affect predation rates has been demonstrated by numerous avian studies (e.g., Tinbergen et al. 1967). Page et al. (1983) presented experimental evidence that low nest density was an important antipredator strategy for Snowy Plovers (*Charadrius alexandrinus*) nesting in homogeneous beach habitat.

We saw few broods in uplands, but our data are probably biased by the greater difficulty of seeing chicks in upland habitats versus wetlands. We strongly suspected that broods made frequent use of uplands during the first 2 weeks after hatching. The broods we observed used taller upland cover than adults alone, presumably gleaning invertebrates from the vegetation and using the taller vegetation as escape cover. Use of wetland habitats by young chicks may be limited by their small size, which results in reduced foraging efficiency, or by their inability to avoid predators in wetland habitats.

The Prairie Pothole ecosystem has been substantially altered by land-use changes associated with the arrival of European culture in the late 1800s. The major environmental changes have been the drainage of wetlands, conversion of native grasslands to small grain and row-crop agriculture, replacement of native grazers with domestic livestock, and suppression of wildfires. No data on Willet population levels in the pristine prairie ecosystem are available, but substantial reductions in historical times are suspected, probably as the result of habitat destruction. The Willet has been extirpated from Iowa and Minnesota (AOU 1983), and range reductions are known in North Dakota (Stewart 1975).

The drought of 1980 and 1981 disproportionately reduced the availability of shallow, less permanent wetlands (Ryan et al. 1984) (Table 1). The temporary loss of these preferred feeding habitats probably was the primary cause of the observed decline in breeding Willets from 1979 to 1981. Small shallow ponds are the most easily drained for agricultural development. As wetland drainage continues in the northern prairie region, Willet populations likely will decline.

Our data suggest that Willets avoid intensively tilled lands. Agricultural development undoubtedly has had a negative impact on the Willet population in the northern Great Plains. Continued conversion of native grass habitats to croplands or nonnative vegetation likely will reduce Willet densities and distribution in this region. Such development will increase the role that publicly managed lands must play in the conservation of Willets and other prairie fauna.

In the Prairie Pothole region, Willets are adapted to exploit short, sparse cover in wetland and upland habitats. In the pristine prairie, these habitat conditions were created and maintained by the interaction of soil moisture, fire, and native grazers (Ryan et al. 1984, Ryan 1986). Management of public wildlife areas in the northern prairie region has been directed primarily at species requiring tall, dense nesting cover. Elsewhere (Ryan et al. 1984, Ryan 1986), we have suggested using grazing, mowing, and prescribed burning on some public areas to assure that all components of the pristine prairie ecosystem, to which grassland wildlife have adapted, are provided. We reemphasize those recommendations.

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THIRD NORTH AMERICAN CONFERENCE ON LOON RESEARCH AND MANAGEMENT

The North American Loon Fund announces the Third North American Conference on Loon Research and Management to be held in cooperation with the Cornell Laboratory of Ornithology on 18 and 19 Sept. 1987 in Ithaca, NY. The Loon Fund invites both papers and posters about loon research and management. For guidelines for submission of papers, contact Dr. Judith McIntyre, Dept. of Biology, Syracuse University at Utica, Utica, NY 13502. For other information and registration materials, contact Scott Sutcliffe, Laboratory of Ornithology, 159 Sapsucker Woods Rd., Ithaca, NY 14850, (607) 255-4288.

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WITHIN-BROOD VARIATION IN GROWTH AND CONDITION IN RELATION TO BROOD REDUCTION IN THE AMERICAN WHITE PELICAN

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Abstract.—Loss of the second (B) chick in broods of American White Pelicans (*Pelecanus erythrorhynchos*) is common and has been attributed to starvation caused by sibling harassment. To examine this possibility in detail, we obtained weekly measurements of body weight and culmen length of individually marked A and B chicks from 80 nests sampled from seven subcolonies on three lakes in Manitoba, Canada, during the period when brood reduction normally occurs (first 2–3 weeks). Over half of the B chicks but none of the A chicks had bruises on the back or head. By the third measurement period, only 14% of the B chicks were alive, compared with 88% of the A chicks. Body size, weight, growth rates, and condition index (weight : culmen ratio) of the B chicks were all depressed relative to the A chicks. Evidence was obtained that B chicks succumbing within a given week weighed less and had smaller condition indices at the start of that week than did those that survived. Condition indices, which can be expected to reflect current food intake levels, exhibited greater within-brood disparity (A > B) for broods in which the B chick was about to die. Results are interpreted as supporting the hypothesis that socially induced food deprivation is causally linked to brood reduction in this species. *Received 30 July 1986, accepted 28 Nov. 1986.*

The American White Pelican (*Pelecanus erythrorhynchos*) characteristically produces a clutch of 2 eggs (Palmer 1962), but rarely fledges more than one young per brood in any given year (Johnson and Sloan 1978, Knopf 1979, Cash and Evans 1986). Brood reduction, which normally occurs during the first 3 weeks after hatching, has been attributed primarily to starvation resulting from harassment of the later hatched smaller chick by its older sibling (Johnson and Sloan 1978, Cash and Evans 1986). Extensive bruises on the head and back of the smaller sibling at many nests (Cash and Evans 1986) attest to the severity of sibling pecks. As a result of these interactions, the smaller sibling is usually driven towards the back of the nest, away from the parent's bill and food. Only the larger young receives food at most feedings (Johnson and Sloan 1978, Cash and Evans 1986). Correlated with this disparity in feeding is a difference in growth of the 2 chicks within a brood.

Despite the hypothesized role of socially induced starvation as a cause of mortality in young white pelicans, quantitative measurements of growth rates and condition indices (Owen and Cook 1977), which would presumably reflect differential food intake, have not been reported. Here we

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compare growth and condition within broods of pelicans over the period when brood reduction normally occurs.

METHODS

Pelicans were studied in 1984 at 3 breeding colonies, East Shoal Lake, Dog Lake, and Kawinaw Lake; all in the interlake region of south-central Manitoba, Canada (see O'Malley and Evans 1980 for map and further description of colonies). To determine the start of nesting activities and to obtain an estimate of hatch onset, colonies at East Shoal Lake were monitored, from shore, two to three times weekly during the period of colony occupation in April (Evans and Cash 1985). This procedure enabled us to delay entering the colonies until the onset of hatch, thereby keeping disturbance to a minimum. Colonies at East Shoal and Dog lakes were visited weekly thereafter, from 4 to 25 June. One final visit to East Shoal Lake was made on 9 July. Kawinaw Lake was visited only once, on 14 June.

White pelicans normally breed synchronously within subcolonies, with greater variation between subcolonies (Knopf 1979, O'Malley and Evans 1980). Subcolonies were therefore selected as sampling units. Each subcolony was chosen to provide a large sample of nests with two young, as near to their date of hatch as possible. To permit assessment of growth at successively later times during the normal breeding season, one new subcolony was selected during each of the first three weekly visits to East Shoal and Dog lakes. Three separate subcolonies were sampled during the single visit to Kawinaw Lake. Fifteen nests were sampled at each subcolony with the exception of one subcolony at Dog Lake, where only 5 nests containing two young were available when it was first visited.

Nests from which measurements were to be taken at East Shoal and Dog lakes were marked with a numbered wooden stake, and a small monel metal web tag (size #1, National Band and Tag Co., Newport, Kentucky) was placed on a foot web of each nestling to permit individual identification on subsequent visits. Measurements of chicks were taken at the time they were marked and again on two subsequent visits, for a total of three measurement dates per bird. During the single visit to Kawinaw Lake, the untagged young were measured once. At all locations, the presence or absence of bruises on the back or head of each young was noted during the first measurement period.

To measure body weight, an individual was slung, with a noose attached to both legs, beneath a pesola scale of appropriate size (minimum accuracy ±5%). As an additional measure of size and growth, culmen length was measured with a ruler to the nearest mm. To permit comparison of body energy reserves in young of different sizes, a condition index (Owen and Cook 1977) was calculated by dividing the square of body weight by culmen length, the result being expressed as a dimensionless value.

The larger chick in each nest at the time of first measurement was designated the A chick, the smaller one the B chick. Because of hatching asynchrony within the brood, these designations normally reflect the true hatching order of the two young within a given nest (Cash and Evans 1986).

Average age of the young from each subcolony was estimated by back dating, using mean body weight of the A chick in each brood as the criterion. Mean body weight at hatching was taken as 110 g (determined from 9 laboratory-hatched young taken from their nest sites at or near the pipping stage). Mean weight gain per day was estimated from the growth rates of a group of 5 colony-reared young whose weight at the time of first measurement (90–120 g, mean = 109 g) was similar to the newly hatched young measured in the laboratory. These colony-reared young were then assumed to be in their first day when first measured. They gained 75 g/day over the first week, and 170 g/day during the second week. Weight gain in pelicans is not always a reliable indicator of chick age, due to variable growth rates that

reflect variable food intake (Schreiber 1976). In the present study, variability was minimized by restricting age estimates to the A chick in each brood, and by obtaining age estimates as soon after hatching as possible. Thus the ages given below are approximate, not necessarily exact.

Starting at about the third week of life, young white pelicans begin to leave their nests and form larger groups, or creches (Evans 1984). Due to increased mobility of older young and associated risks of colony disturbance at that time, measurements were discontinued prior to young reaching their asymptotic weights and probably prior to their reaching the inflection point on the growth curve (cf. Schreiber 1976). It was therefore not possible to analyze growth by means of conventional growth curves (the assumptions required for computing growth curves from single visits were not met, cf. Ricklefs and White 1975). To analyze growth, we determined mean growth per day for each young over a given weekly interval between two successive measurements. Differences in growth were assessed by analysis of variance (ANOVA) and, where appropriate, *t*-tests.

RESULTS

Eighty-eight percent of the 80 web-tagged A chicks survived at least until the third measurement period. Survival was significantly lower for the 80 B chicks in the same nests ($\chi^2 = 75.4$, df = 1, $P < 0.001$), with only 14% surviving over the same period. No evidence was obtained to suggest that differential loss of web tags rather than mortality accounted for the drop in numbers between weeks. Of the 160 young at marked nests, only 2 were found with perforated web but no tag.

In the 80 nests initially marked, both young survived up to the third measurement period (>2 weeks of age) at only 8 nests (10%). The B chick became larger than the A chick at one of these 8 nests. The B chick, rather than the A chick, survived to the third measurement period at 2 additional nests. Bruises on the head or back were noted on 69 of 125 B chicks (55.2%, includes data from Kawinaw Lake visit) at the time of first measurement. None of the A chicks had visible bruises at that time.

The pattern of growth was similar at all subcolonies (Fig. 1) (Table 1). To test for growth differences among subcolonies across age levels, the mean daily growth rates at 3 subcolonies having similarly aged young at the time of first measurement (subcolonies 2 and 3 on East Shoal Lake and subcolony 3 on Dog Lake) were compared for A chicks with 2-way ANOVA with repeated measures on one variable (successive weeks). The other variable was the three different subcolonies included in this analysis. Differences between subcolonies were not significant for either body weight ($F = 0.29$; df = 2,36; $P > 0.05$) or culmen length ($F = 0.36$; df = 2,36; $P > 0.05$). Interaction between age and subcolonies was significant only for body weight ($F = 6.06$; df = 2,36; $P < 0.01$). Age differences were significant for increases in both body weight ($F = 162.9$; df = 1,36; $P < 0.001$) and culmen length ($F = 4.28$; df = 1,36; $P < 0.05$), with older young growing faster in each case. Subsequent *t*-tests indicated that in-

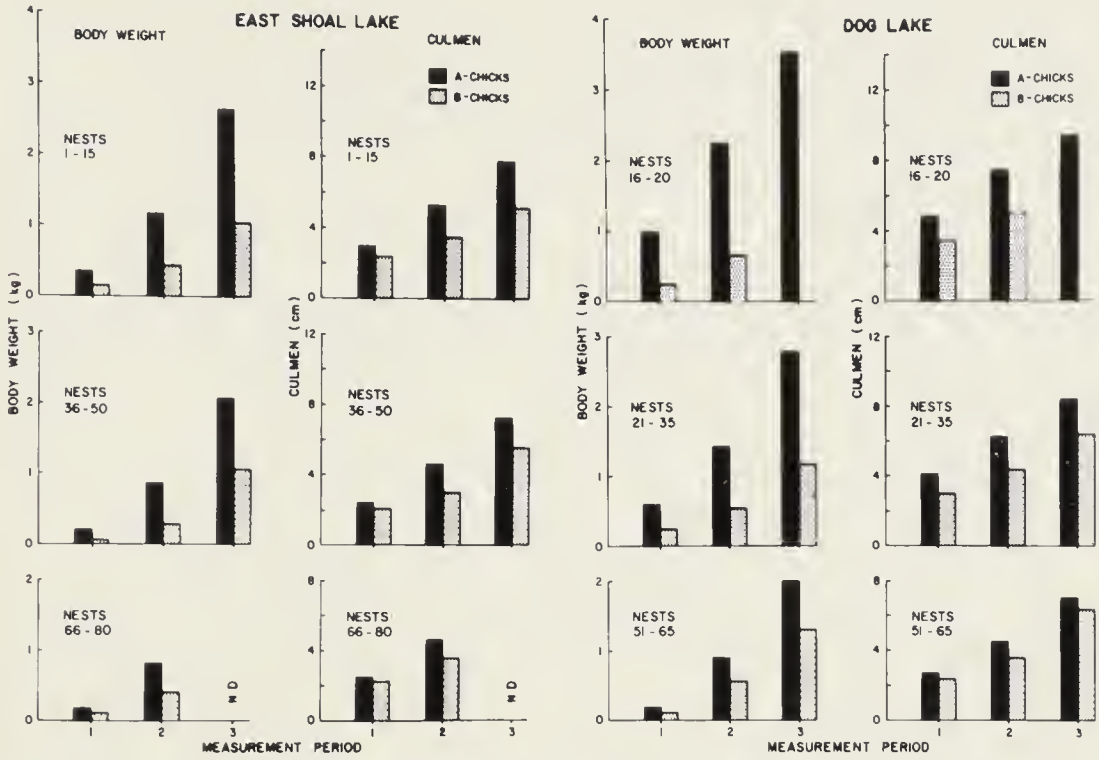

FIG. 1. Mean body weight and culmen length over three measurement periods for subcolonies at East Shoal Lake and Dog Lake. ND = not measured.

creasing growth rate with age was present for body weight at each of the three subcolonies included in the ANOVA and was also present ($P < 0.001$) at each of the remaining subcolonies that had been excluded from the ANOVA because they were older when first measured (Table 1).

Differences in growth with age were less consistent for culmen length. Only one of the three subcolonies included in the ANOVA showed significant age differences in growth rate ($t = 3.47$, $P < 0.01$). One of the subcolonies excluded from the ANOVA showed a significant effect of age ($t = 2.83$, $P < 0.02$), but the other did not ($P > 0.05$). Although there were some differences in growth rates between subcolonies, they were not sufficiently consistent to produce a significant main effect, and all subcolonies were combined for subsequent analyses.

For 9 B chicks that survived for all three measurement periods, mean daily increase in body weight was less during the first week than during the second week (51.0 vs 80.3 g/day), but the difference was not statistically significant ($t = 1.42$, $P > 0.05$). For culmen length, growth rate during the first week (1.9 mm/day) was significantly less than during the second week (2.7 mm/day: $t = 2.91$, $P < 0.02$).

Average growth rates suggest that the A chicks typically grew at a faster rate than did B chicks (Table 1). Direct comparison of A and B chicks present at 26 nests during both the first and second measurement periods

TABLE 1

MEAN [±SD] GROWTH RATES FOR BODY WEIGHT AND CULMEN LENGTH OF YOUNG AMERICAN WHITE PELICANS AT SIX SUBCOLONIES IN 1984

Subcolonies	Date[a]	Age of chicks (days)	Number of chicks[b]		Weight (g/day)		Culmen (mm/day)	
			A	B	A	B	A	B
East Shoal								
1	4, 11 June	4, 11	11	5	117 ± 36	33 ± 19	3.2 ± 0.4	1.3 ± 0.1
	11, 18 June	11, 18	11	3	215 ± 51	71 ± 20	3.6 ± 0.3	2.2 ± 0.1
2	11, 18 June	2, 9	15	6	96 ± 14	26 ± 17	3.2 ± 0.3	1.4 ± 0.5
	18, 25 June	9, 16	15	3	171 ± 25	94 ± 3	3.6 ± 0.5	3.1 ± 0.6
3	18, 25 June	2, 9	14	9	88 ± 25	34 ± 20	3.2 ± 0.8	1.9 ± 0.7
	25 June	9, 23	14	ND[c]	169 ± 31	ND	3.4 ± 0.3	ND
	9 July							
Dog Lake								
1	4, 11 June	10, 17	5	1	178 ± 32	33	3.7 ± 0.8	1.3
	11, 18 June	17, 24	5	0	183 ± 74		2.7 ± 0.8	
2	5, 12 June	8, 15	15	6	121 ± 35	40 ± 44	3.1 ± 0.5	1.9 ± 0.9
	12, 18 June	15, 21	15	3	218 ± 89	76 ± 125	3.6 ± 0.8	2.8 ± 1.0
3	12, 18 June	2, 8	13	3	108 ± 34	43 ± 14	3.2 ± 0.7	1.8 ± 0.7
	18, 25 June	8, 15	10	0[d]	152 ± 37		3.4 ± 0.3	

[a] Growth rates calculated from measurements taken on the pairs of dates indicated.

[b] Fifteen A and 15 B chicks were measured during the first visit at all subcolonies except at Dog Lake subcolony 1, where only 5 pairs were available. Number of chicks shown here represents number still alive and sampled on both of the indicated measurement dates.

[c] ND = chicks inadvertently not measured.

[d] One nest with a B but no A chick excluded from growth rate analyses. Measurements for this bird are included in Fig. 1.

indicated that the difference was statistically significant (body weight: $t = 11.04$, $P < 0.001$; culmen: $t = 9.24$, $P < 0.001$). Only 8 pairs of comparisons could be made between the second and third measurement periods due to mortality in the B chicks. Growth rates of the surviving B chicks at this age did not differ significantly from their sibling A chicks (body weight: $t = 2.16$, $P > 0.05$; culmen: $t = 1.54$, $P > 0.05$). Prior growth rates, between the first and second measurement period, for this same subsample of 8 nests followed the overall trend, in that growth of the B chicks was significantly less than the A chicks at that time (body weight: $t = 3.70$, $P < 0.01$; culmen: $t = 4.18$, $P < 0.01$). These results indicate that the initial disparity in growth rates between A and B chicks eventually becomes less severe at those nests where both chicks survive past the initial, and most intensive, period of brood reduction.

In the above analyses, body weight and culmen length tended to be similarly affected (Fig. 1), suggesting a strong correlation between these two measures. Inspection of young in the colony, however, suggested that the ratio of body weight to culmen length could be quite different among the young. In particular, B chicks appeared to be less plump, and often somewhat emaciated. This should result in a lower condition index, i.e., lower body weight relative to a linear measurement such as culmen length. For the first two measurement periods, condition indices were significantly less for the B chicks (Table 2). Mean values were not significantly less for the B chicks at the third measurement period, due primarily to a size reversal in one of the eight pairs measured at that time. Results for the single visit to Kawinaw Lake (Table 2) provided further evidence that condition indices of the A chicks were normally greater than those for the corresponding B chicks. Reduced indices for the smaller chicks (in all but one case the B chick) is consistent with the interpretation that the high mortality rates present in these young is related to reduced food intake.

If mortality in B chicks is causally related to loss of weight and starvation, then, of the B chicks alive in a given week, those that succumb during the immediately following week should show evidence of reduced growth compared with those B chicks that survive at least to the end of that week. Relevant measurements were obtained for 57 B chicks (Fig. 2). Those that succumbed between the first and second measurement periods (bars with diagonal lines) were less heavy and had smaller culmens when first measured than those that survived past the second period, but differences were not statistically significant (t-tests, $P > 0.05$). Differences at the time of the second measurement period were greater. B chicks that died between the second and third measurement period (open bars) were significantly lighter during the second measurement period than were those that survived past the third period ($t = 2.30$, $P < 0.05$). A similar,

TABLE 2
MEAN [±SD] CONDITION INDICES FOR A AND B CHICKS AT NESTS CONTAINING TWO YOUNG WHEN MEASURED

Measurement period	No. pairs measured	A chick	B chick	t	P
1[a]	80	0.57 ± 0.07	0.48 ± 0.06	10.81	<0.001
2	26	0.63 ± 0.04	0.52 ± 0.09	6.21	<0.001
3	8	0.61 ± 0.05	0.55 ± 0.03	1.91	0.1>, >0.05
Kawinaw Lake	45	0.59 ± 0.04	0.47 ± 0.06	9.93	<0.001

[a] See Table 1 for measurement periods for East Shoal and Dog lakes.

but not significant ($P > 0.05$), difference was present for culmen length. Although small sample sizes of B chicks surviving past the first measurement period preclude unequivocal conclusions, the results for older chicks suggest that a correlation exists between an individual's weight and its probability of survival.

If mortality in B chicks is related to weight loss and starvation, then condition indices should be less for those chicks that succumbed during a given week than for those that survived. The mean index value for 38 B chicks that perished before the second measurement period was 0.46, less, but not significantly so, than for the 19 B chicks that survived ($\bar{x}$ = 0.50). For the 10 B chicks that succumbed between the second and third periods, the mean index value was 0.47 at the time of the second measurement period compared with 0.59 for the nine B chicks that survived past the third period ($t = 3.51$, $P < 0.001$).

Another relevant comparison is the difference in magnitude of condition indices between A and B siblings, a greater disparity within the brood being expected for broods in which the B chick is about to die. There was no significant difference ($P > 0.05$) in this value for young that succumbed between the first and second periods, but the effect was significant in broods where the B chick succumbed between the second and third measurement periods. For these older young, the mean difference in condition index values was 0.17 for the 10 broods in which the B chick did not survive until the next period, compared with only 0.05 for those broods in which the B chick did survive ($t = 3.36$, $P < 0.01$). In these older young there appeared to be a greater within brood disparity in food intake, as reflected in condition indices, for broods in which the loss of the B chick was imminent.

DISCUSSION

In agreement with several earlier studies (Behle 1958, Schaller 1964, Johnson and Sloan 1978, Knopf 1979, Cash and Evans 1986), brood

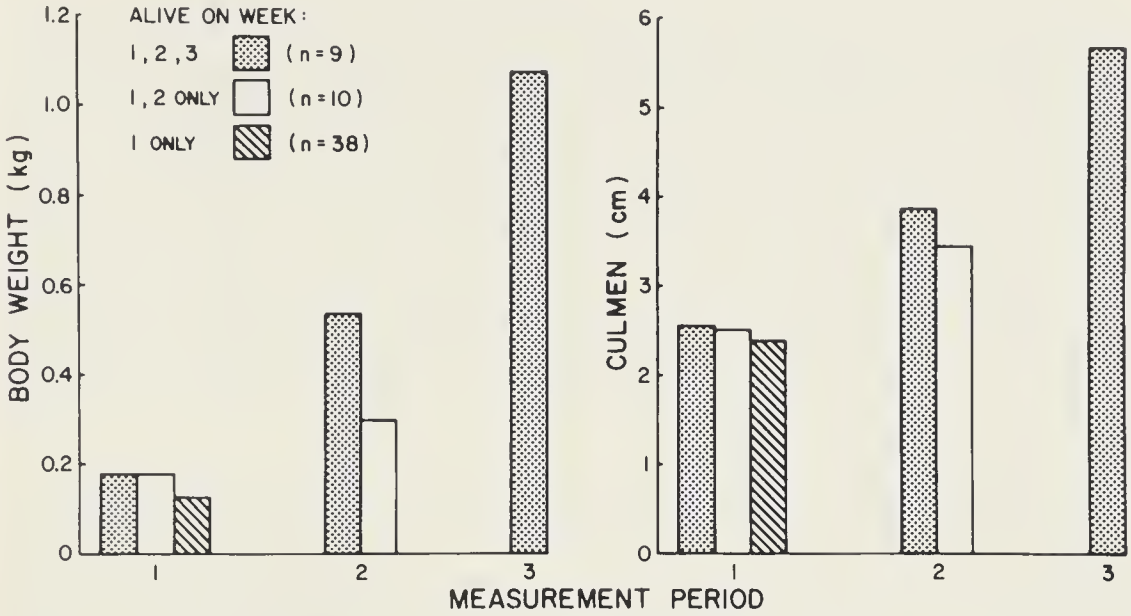

FIG. 2. Mean body weight and culmen length for B chicks that survived through measurement periods 1, 2, or 3.

reduction within the 80 marked nests sampled in this study was severe, with a maximum of 14% of B chicks surviving to the third measurement period (approximately 2 to 3 weeks of age). In contrast, survival of the A chicks over the same age was high (88%). Because mortality rates in this species tend to drop to low levels once the creche stage is reached at 2 to 3 weeks (Knopf 1979, Evans 1984), the results indicate that most breeding pairs fledged one young. This level of productivity is similar to that reported at East Shoal Lake in an earlier study (Cash and Evans 1986), but appreciably greater than reported in some other colonies (Johnson and Sloan 1978, Knopf 1979).

Mean growth rates for A chicks were similar among the subcolonies, and in most instances they exhibited a characteristic increase during the presumed exponential phase of the growth curve. A weekly increase in growth rates over the first three weeks has also been reported in the Brown Pelican (*P. occidentalis*) (Schreiber 1976). Relatively stable growth rates and high survivorship among the A chicks suggest that food supplies for the study populations were adequate for one-chick broods throughout the time of the study. Recent population increases in these and other colonies in this region (cf. Evans 1972, Evans and Cash 1985, Koonz and Rakowski 1985) support this conclusion. All of the populations in the study foraged extensively in one or both of two large lakes, Lake Winnipeg and Lake Manitoba, which evidently provided an adequate food supply at this time. Populations relying on smaller lakes for food may be subject to greater fluctuations in food availability and may experience greater fluctuations in reproductive output (Johnson and Sloan 1978).

The smaller size, significantly reduced growth rates, and smaller condition indices of the B chicks, combined with back or head bruises and high mortality rates in this group, all point to socially induced food limitation as a causative agent in brood reduction in this species. The tendency for B chicks that succumbed between the second and third measurement periods to be less heavy and have smaller condition indices than those B chicks that did not succumb during the same period provides further support for this interpretation. Also, most of the brood reduction in the marked sample of nests occurred between the first and second measurement periods, when growth rate differences between A and B chicks were most pronounced.

Between the second and third measurement periods, differences in growth rate between the A and B chicks did not reach statistical significance. Although the sample size was small for this comparison due to prior brood reduction, the results indicated that surviving B chicks did relatively better at obtaining food as they got older, provided they were able to survive the initial period of intense mortality. The similarity in condition indices within broods in which both young survived up to at least the third measurement period also suggests that the surviving B chicks were obtaining more food at that time. An increased ability of surviving older B chicks to obtain more food could account for instances (e.g., Knopf 1979) where both young fledge.

Although lack of food appears to be a strong correlate and probable causative agent in mortality of B chicks, starvation is not necessarily the immediate cause of mortality. As described elsewhere (Cash and Evans 1986), movement of the smaller chick to a more exposed position within or beyond the nest could result in death from exposure or from pecks delivered by neighboring adults. In some instances, the B chick is sufficiently harassed by its sibling that it is driven out of the nest, where it can fall prey to gulls (Evans 1984). In all of these instances, the action of food deprivation is presumably indirect, causing the chick to be more vulnerable to exposure, attack, or to being driven to a less safe location.

According to the interpretations of brood reduction developed by Lack (1954), selective mortality of the youngest sibling(s) is assumed to be due to an inability on the part of the parents to deliver sufficient food to the nest to feed all young adequately. Most evidence to date appears to support this interpretation (O'Connor 1978, Mock and Parker 1986, but see Clark and Wilson 1981 for a critique). In pelicans, it is also possible that parents are unable to deliver adequate amounts of food at the time brood reduction occurs, but direct evidence for this interpretation has yet to be produced. Direct evidence that parents are able to provide adequate food to the young nestlings is also lacking, but indirect support for this interpretation

comes from the timing of brood reduction which occurs during the first two weeks of age (Johnson and Sloan 1978; Cash and Evans 1986, this study), at a time when the young are still small (Fig. 1) and require relatively small amounts of food. Boluses of food observed being fed to older, creche-aged young typically are larger than the entire body size of the young at the time most brood reduction is occurring (Evans, pers. obs.). These considerations suggest that low levels of food intake by the B chick result mainly from behavioral causes, primarily the pecking and harassment by the A chick that causes the B chick to move towards the rear of the parent, combined with the tendency of the parent to passively feed whichever young is foremost in the nest (Cash and Evans 1986). Brood reduction at an early age in Blue-eyed Shags (*Phalacrocorax atriceps*) (Shaw 1985) has similarly been attributed to behavioral causes rather than to environmental limitations on food availability. In American White Pelicans, the presence of bruises on the head or back of over half of the B chicks but on none of the A chicks supports the conclusion that sibling harassment is prevalent and correlates strongly with lower growth and higher mortality in the B chicks.

To the extent that food limitation in B chicks results from dominance-related behavior between the siblings, initial size disparity can quickly accelerate as the smaller, underfed sibling becomes even less effective in aggressive interactions. This positive feedback arising from interactions among food, body size, and dominance status provides a plausible explanation for the rapidity with which B chicks can fall behind in overall growth, as well as for the rapidity with which brood reduction can occur.

Socially induced starvation within broods is rare in birds, but it is exhibited in other species in which brood reduction occurs well before the time that food might become limiting as the young grow larger (Shaw 1985, reviewed in Mock 1984). The possibility that white pelicans would normally be unable to feed both young throughout the creche stage when food demands become greater is also unproven, but the intense begging exhibited by single chick broods at that time (Cash and Evans, in press) suggests that food delivery by the parents to older young is not excessive. If so, elimination of a potential rival sibling at an early age would appear to be an adaptive strategy on the part of the dominant A chick, even though food may be abundant at the time brood reduction is effected.

In a recent study of brood reduction in Great Egrets (*Casmerodius albus*) and Great Blue Herons (*Ardea herodias*), Mock and Parker (1986) suggested that reproductive value, RV, of the youngest sibling(s) be divided into two components: that due to the production of an additional unit of reproductive success (RV_e; i.e., in pelicans, both A and B chicks survive), and that due to replacement of the older sibling, the so-called insurance

option (RV_i; i.e., in pelicans, the B chick survives at nests where the A chick dies). At the time of the final measurements in the present study, maximum possible RV_e for B chicks was 0.11, while maximum possible RV_i was only 0.03. Because there were still large differences in body size between the A chicks and remaining B chicks at the time of our last measurements (Fig. 1), further brood reduction could have occurred that would have reduced RV_e below the value of 0.11. In a previous study (Cash and Evans 1986) at one of the same colonies (East Shoal Lake), we found that only the B chick survived at 9 of 50 marked nests and that no nests produced more than one young. Calculations based on these figures give an RV_i of 0.18, and an RV_e of zero. Other studies (Johnson and Sloan 1978, Knopf 1979) provide no data with which to calculate RV_i values, but indicate that up to at least 10% of nests in some regions may produce two offspring. This would give an RV_e value of 0.10, similar to the maximum possible RV_e obtained in the present study. In general, the total RV of white pelican B chicks appears to be lower than for the youngest siblings in broods of herons or egrets (cf. Mock and Parker 1986).

ACKNOWLEDGMENTS

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RAPTOR RESEARCH FOUNDATION MEETING

The Raptor Research Foundation is an organization whose purpose is to stimulate the dissemination of information concerning raptorial birds among interested persons worldwide and to promote a better public understanding and appreciation of the value of birds of prey. Towards this objective, we are holding our annual meeting on 28–31 October 1987 at Boise, Idaho. The meeting will feature a symposium on the migration of raptors in western North America. General paper and poster sessions will follow the symposium. The Conference Committee Chairperson is Rich Howard, U.S. Fish and Wildlife Service, 4696 Overland Rd., Rm. 576, Boise, Idaho 83705 (Phone number 208/334-1888).

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HABITAT USE AND TERRITORY CHARACTERISTICS OF RED-COCKADED WOODPECKERS IN CENTRAL FLORIDA

Roy S. DeLotelle,[1] Robert J. Epting,[1] and James R. Newman[2]

Abstract.—Habitat use and territory characteristics of six groups of Red-cockaded Woodpeckers (*Picoides borealis*) were studied in central Florida at the southern margin of the species' range. Compared to more northerly habitats, pine stands were lower in density, younger, or of smaller size class. A suite of foraging patterns compensates for the resource-poor habitat. An analysis of population density and available habitat indicates that Red-cockaded Woodpeckers in central Florida require larger territories and are more sensitive to population pressure in poorer-quality habitat. These results indicate that minimal territory size may vary depending on the quality of the habitat. A regression model of stand size, territoriality, cavity tree location, and stand structure effects accounts for 93% of pine stand use. Sensitivity analyses of model components indicate that, after the effect of stand size, stand use is most sensitive to the effects of territoriality, followed by stand age, stand density, and cavity-tree location. Thus, stand use depends simultaneously on the distance of the stand from the cavity trees and territorial interaction sites and pine stand age and density.
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The Red-cockaded Woodpecker (*Picoides borealis*) is endemic to pine forests of the southeastern United States and is currently considered endangered because of loss of habitat. Red-cockaded Woodpeckers are nonmigratory and occupy territories that are defended year round and that contain nest sites and foraging habitats. Nesting habitat is associated with mature (≥70 years) pine, whereas foraging habitat is more variable and includes a broader range of age classes (Lennartz and Henry 1985).

Factors affecting habitat use and territory characteristics have been studied thoroughly in South Carolina near the middle of the species' distribution (Hooper et al. 1982, Lennartz and Henry 1985). Habitat use and home range characteristics have been described for populations in central and south Florida at the southern margin of the species' distribution (Nesbitt et al. 1978, 1983; Patterson and Robertson 1981). Compared to more northerly populations, habitats used by southern birds are of poorer quality (less dense and smaller size trees), and Nesbitt et al. (1983) suggested that habitat quality is important in determining home range size. No previous study has quantitatively evaluated the influences of population pressure and habitat quality on populations at the southern margin of the species' range in poor-quality habitats. Furthermore, the

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relative importance of pine stand age, density, territoriality, and cavity-tree location on foraging ecology has not been analyzed. This paper evaluates factors affecting habitat use and territory characteristics for six groups of Red-cockaded Woodpeckers from central Florida and compares this resource-poor population to more northerly populations occupying better habitat.

METHODS

The 1328-ha study area, the Curtis H. Stanton Energy Center, is 21 km southeast of Orlando, Florida. Observations were conducted for 2 years, beginning in the fall of 1980, on group movements during the fall (September–December); winter (January–March); and summer (June–August) (DeLotelle et al. 1983). A total of 722 h of observations was made on six groups in the study area (Group A: 150 h; Group B: 75 h; Group C: 150 h; Group D: 149 h; Group H: 152 h; Group G: 46 h), averaging 7.8 h of observation per day. An additional 17 groups (1 group per 139 ha) occupied surrounding habitat. As suggested by Nesbitt (pers. comm.), groups were usually observed from morning to well into the late afternoon to ensure that we had observed the farthest point from the cavity trees the birds had reached on foraging trips. On other occasions groups were followed from near noon to roosting.

Here, we use the more traditional definitions of territory and home range (Burt 1943) to describe the defended area and total foraging range, respectively. The above two terms are analogous to home range and total observed range, respectively, used by Hooper et al. (1982) (Hooper, pers. comm.). Movements of groups, marked with color-coded plastic leg bands (N = 27), were recorded at 5-min intervals on photocopies of aerial photographs (scale 1:4800). Home ranges were estimated by connecting peripheral points of group movements. Group interactions were recorded on the photocopies, and territorial boundaries were determined following the procedure of Hooper et al. (1982). Territory size and configuration were based primarily on the locations of territorial boundaries. No territorial interactions were observed in certain segments of the home range. These areas were deleted from the territory if they were visited only once by the resident group. Disputes as determinants of territorial boundaries, and thus territory size, have been used in many avian studies (Myers et al. 1979, Hooper et al. 1982). Although Groups B and G were observed for fewer hours, each of these two groups shared three territorial boundaries with other groups studied. Interactions were observed involving Groups B or G with their neighbors along these shared boundaries, thus providing reliable estimates of their territory configurations.

Vegetation characteristics, including pine stand age and density, were determined by DeLotelle et al. (1983). A 1-in.^{2} grid, representing a 1.5-ha plot, was traced on the aerial photographs, from which 72 grids were analyzed for tree density using a Leitz MS-27 2× and 3× stereoscope. Twenty-five plots were field-inspected for dbh, tree density, age, and basal area. Territory configurations were superimposed on the site vegetation map to obtain the stand characteristics of each territory. Stand use was determined by summing all observations for a particular pine stand.

To evaluate the effect of population density on territory size, territory size was regressed against area of suitable habitat within a 2000-m radius of cavity trees of each group divided by population density within the area (i.e., mean available habitat per group) (Hooper et al. 1982). Suitable habitat included all pine forests and all small cypress stands with all clearcuts and hardwood swamps excluded. Central Florida and South Carolina populations (Hooper et al. 1982) were compared using a 2-sample t-test for slopes of regression lines.

Indices of the influences of cavity-tree location and territorial behavior on stand use were

measured as the distances from the midpoint of each stand to the cavity trees and the focal point of territorial activity, respectively. For each group, the focal point of territorial activity represented the mean of the coordinates for all observed group interactions. The midpoint of cavity-tree location was taken from DeLotelle et al. (1983). Cavity tree and territory distances were standardized by dividing by the average diameter of each territory.

Observed stand use, expressed as a percent of total foraging within the entire territory, was regressed against stand size using SAS (SAS Institute 1985). The residuals (observed minus predicted stand use) from this regression are independent of stand size and are used in further analysis (Afifi and Clark 1984). A regression model of differential stand use (observed stand use residuals) was constructed employing distance from the cavity-tree location to the midpoint of each stand, distance from the territorial focal point to the midpoint of each stand, and pine stand structure. Differential stand use as a dependent variable is not the same as stand preference based on use-availability ratios used elsewhere (see Wood et al. 1985).

Several procedures were used to solve violations of the nonlinearity, interaction, and multicolinearity assumptions of multiple linear regression. The natural logarithmic transformation was performed on stand characteristics, including age, density, and dbh. An interaction term often takes into account the non-additive effects of two regression factors (Afifi and Clark 1984). We evaluated a cavity-tree distance times territory distance (see above) interaction term and age or dbh times density interaction term. The model variables were then subjected to principal component analysis to remove the effects of multicolinearity. The principal component analysis used the correlation matrix which is equivalent to the use of standardized variables and allows the direct interpretation of the principal component loadings (Afifi and Clark 1984).

Evaluation of alternative models and transformations was based on plots of adjusted R^2 versus the number of variables in the model and on plots of residuals versus each of the regression factors in a given model. For models with the same number of regression factors, model selection was based on the best subset regression method (Afifi and Clark 1984).

To perform the sensitivity analyses, two regression equations of the original variables were obtained by multiplying the loadings for each principal component by their respective multiple regression parameters and re-collecting terms in original variable order. The two graphical sensitivity analyses, employing the standardized regression equations, were stand age versus density and territory focal point versus cavity-tree location at given levels of differential stand use. In both solutions the remaining variables were set to their mean values. Because of the use of the correlation matrix in the principal component analysis, the mean value of all variables is zero, so that only the pair of variables of interest remain in the solution to the regression equation. The whole-model sensitivity analyses solved the regression equation for the variable of interest and then varied each variable by a fixed amount (Smith 1970). The intercept form of the regression equation was obtained from the standardized equation by factoring the original variable means and standard deviations from the regression coefficients.

RESULTS

Home range and territory use.—Group activity during daily foraging movements was similar to that reported by Nesbitt et al. (1983). This included a congregation period in the morning accompanied by much vocalization and flying about the cavity tree stand. Normally, group members followed a regular pattern consisting of a foraging trip away from the

TABLE 1

TERRITORY SIZE, AVAILABLE HABITAT, AND TERRITORIAL BEHAVIOR CHARACTERISTICS OF RED-COCKADED WOODPECKERS ON THE STANTON ENERGY CENTER, FLORIDA

Group	Home range (ha)	Territory (ha)	Number of groups[a]	Available habitat[b] (ha)	Interval between interactions[c] (h)	Focal point distance from cavity tree (m)	Extraterritorial movements: Interval between trips[c] (h)	Extraterritorial movements: Mean length (m)
A	198.8	154.9	4	170.6	30.0	763.2	25.0	368.2
B[d]	157.8	147.0	6	156.6	15.0	586.4	18.8	333.5
C	116.2	101.5	10	103.7	18.8	320.7	18.8	297.8
D	123.1	105.7	10	107.1	14.9	357.2	18.8	190.5
G[e]	ND	92.7	11	93.8	11.5	228.0	15.3	252.4
H	154.2	94.7	9	108.0	11.7	71.7	9.5	220.4
Mean	150.0	116.1	8.3	123.3	17.0	387.9	17.7	277.1
SD	32.9	27.5	2.7	31.9	6.91	249.5	5.1	196.3

[a] Number of groups within 2000-m radius of cavity trees.
[b] Hectares of mean available habitat within 2000-m radius of cavity trees (i.e., total suitable habitat/number of groups).
[c] Indicates the number of hours required to observe either a territorial interaction or extraterritorial movement.
[d] Group B abandoned cavity trees and territory prior to the nesting season in 1982.
[e] No home range data during fall and summer; not included in mean for home range.

cavity trees in the morning with a return to the vicinity of roosting sites later in the day. While in the vicinity of cavity trees, Red-cockaded Woodpeckers were engaged in cavity maintenance, protection of the cavities from intruders, and construction of new cavities. In stands farther from the cavity trees, Red-cockaded Woodpeckers' activities consisted primarily of foraging, resting, and scanning and listening for predators and neighboring groups of woodpeckers. In some of these more distant stands, birds often encountered other groups of Red-cockaded Woodpeckers or initiated forays into their neighbors' habitats.

Home range size averaged 150.0 ha (Table 1). Mean territory size was 116.1 ha and accounted for 77.4% of the mean home range. Habitats within territories consisted of pine flatwoods (88.1%), cypress domes and bayheads (8.6%), and wet prairie and open areas (3.3%). Mean amount of pine flatwoods per territory was 102.3 ha, which included a mean of 9768 pine stems (≥6.0 cm dbh). Mean pine basal area per territory was 267.6 m^2 (range = 204.6–355.8 m^2). Cypress trees constituted about 40% of the total stems and basal area in the territories. Pine stands in the territories (Table 2) consisted mostly of younger trees ranging in age from approximately 17 years to 53 years. An older age class much lower in density and averaging 110 years in age was included in many stands. Of the pine stands in the territories, 59% were logged for pulpwood during

TABLE 2

PINE STAND AND FORAGING PARAMETERS FOR SIX GROUPS OF RED-COCKADED WOODPECKERS ON THE STANTON ENERGY CENTER, FLORIDA

Group	No. stands in territory	Mean stand size (ha)	Mean stand density[a] (ha)	Mean dbh (cm)	Mean age of trees (years)	Mean % time observed foraging	Mean distance of stand from cavity trees (m)	Mean distance of stand from territorial focal point (m)
A	6	20.5 ± 12.0[b]	97.0 ± 86.5	17.4 ± 3.2	46.3 ± 26.1	16.7 ± 14.4	524.6 ± 229.6	770.1 ± 304.9
B	4	32.7 ± 30.6	154.9 ± 118.9	15.4 ± 2.6	34.8 ± 11.1	25.0 ± 25.8	556.7 ± 205.0	741.2 ± 270.1
C	5	19.3 ± 21.1	159.7 ± 131.8	18.1 ± 4.3	48.2 ± 31.7	20.0 ± 14.2	403.6 ± 174.0	495.3 ± 243.9
D	7	12.8 ± 16.0	167.1 ± 110.4	14.9 ± 3.7	45.1 ± 26.5	14.3 ± 18.3	479.0 ± 223.6	397.4 ± 161.8
G	5	17.3 ± 17.5	141.1 ± 111.2	19.9 ± 3.1	56.6 ± 28.3	20.0 ± 24.3	395.0 ± 139.1	384.3 ± 193.4
H	4	20.8 ± 22.6	185.2 ± 135.4	17.9 ± 4.8	52.0 ± 36.7	25.0 ± 24.1	465.5 ± 263.9	385.8 ± 192.1

[a] Includes all pine stems ≥6 cm dbh.
[b] Mean ± SD.

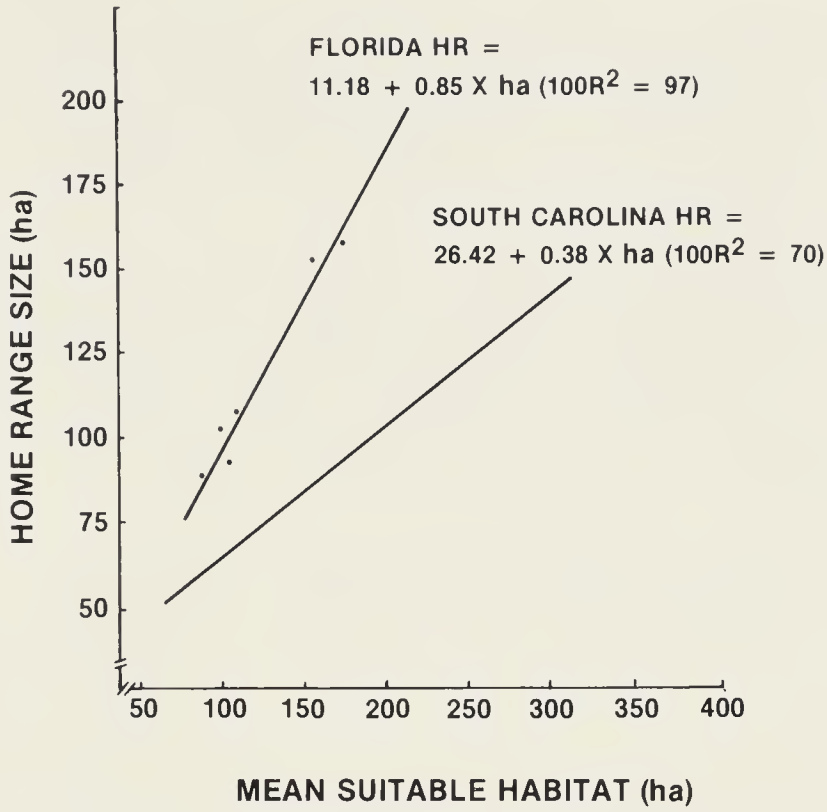

FIG. 1. Comparison of regressions for home range size versus area of mean suitable habitat within 2000 m for central Florida and South Carolina populations; N = 6 for central Florida and N = 24 for South Carolina (Hooper et al. 1982).

the past 10 years and had densities ranging from 32 to 122 stems/ha. The remaining stands were unlogged (densities from 92 to 319 stems/ha) and constituted 41% of the territories.

Territory sizes and surrounding population densities were variable (Table 1). Territories occupied almost all ($\bar{x}$ = 95%; range = 88–99%) of the available habitat, whereas home ranges overlapped and accounted for 119% of available habitat. Furthermore, especially in the denser population areas, home ranges overlapped surrounding territories. Territory size was positively related to the area of suitable habitat within a 2000-m radius of each group of cavity trees ($R^2 = 0.97$, $P < 0.0001$, N = 6). Thus, the relative amount of available habitat accounts for a significant percent of the variation in territory size in the central Florida populations (Fig. 1). Comparison of the two regression lines for central Florida and South Carolina (Hooper et al. 1982) indicates that the response to population density for the central Florida population was higher than in South Carolina and that it had a significantly steeper slope ($P = 0.005$).

Intergroup conflicts occurred throughout the year except when nestlings were present. Of the 45 group interactions, 94% occurred at or near observed territorial boundaries. The remaining 6% occurred well within

territories, usually near the cavity trees. Most group interactions were between closest neighboring groups. The mean number of adjacent groups encountered by each group was 3.6 ± 1.14 [SD]; however, 51% of observed interactions were with a specific neighbor. Thus, the territorial focal point was generally near the territorial boundary with the most frequently encountered neighbor. On several occasions groups were observed to travel up to 950 m from within their territory to intercept an intruding neighbor at the territorial boundary. After interactions, groups usually resumed foraging in nearby stands within their respective territories. There were instances, however, in which territorial boundaries were not respected even when the boundary segment had already been estabished earlier that same day by interacting groups.

In addition, the six groups made a total of 45 forays outside their territories. Of the 45 extraterritorial movements, 37 (82%) were into adjacent territories, and 10 of these were into or approaching neighboring cavity trees. Of the 8 extraterritorial group movements into unoccupied habitat, 75% were into the abandoned territory of Group B and beyond previously observed interaction sites. Mean distance traveled outside the territory was 277.1 ± 196.3 m. The mean distance traveled outside the territory and into unoccupied habitat (465.7 ± 183.8 m) was significantly greater than the mean distance traveled into occupied habitat (217.3 ± 166.0 m) (2-sample t-test, $P = 0.006$).

Habitat use.—Longleaf pine stands were selected for foraging 90% of the time compared with 10% for cypress stands. Cypress domes were important seasonal foraging sites, and their use generally exceeded their availability for most of the study-site groups (10% use vs 6% availability). Small, open-canopied cypress domes (64% of the cypress area) accounted for 89% of the cypress foraging. Unlogged pine stands occupied 41% of the home ranges, but accounted for 59% of the foraging observations. Stand use was significantly correlated with pine stand size (use = 3.87 + 0.79 × size; $R^2 = 0.63$, $P = 0.0001$, N = 31).

The multiple regression (Table 3) of differential stand use on the principal components (PRIN 1–6) of age, density, age times density, cavity-tree location, territorial focal point, and cavity tree times territory was significant ($R^2 = 0.81$, $P = 0.0001$, N = 31). This model accounts for 81% of the 37% (100–63%) variability unexplained by size, so that 93% (63%+ 81% × 37%) of stand use is explained. The large value of adjusted R^2 (0.77) compared to unadjusted R^2 indicates an unbiased regression model and parsimonious choice of variables. Principal Components 1, 2, 4, and 5 are significant, and 3 is nearly significant. The variable loadings for the principal components appear to have readily defined biological interpretations (see Table 3). Cavity-tree location and territoriality are localizing

Table 3
Multiple Regression on Principal Components

	Principal components					
	PRIN 1	PRIN 2	PRIN 3	PRIN 4	PRIN 5	PRIN 6
Proportion	0.4740	0.2705	0.1764	0.0726	0.0060	0.0004
Eigenvectors						
ln D[a]	0.2078	0.7296	−0.0476	−0.1513	−0.0357	0.6310
ln A	−0.3856	−0.3101	0.6170	0.1984	−0.0433	0.5772
ln D*ln A[b]	−0.1733	0.5504	0.6300	0.0672	0.0495	−0.5129
C	0.5057	0.0044	0.0560	0.7790	0.3642	0.0400
T	0.4667	−0.2269	0.3704	−0.5711	0.5162	0.0288
C*T	0.5519	−0.1307	0.2823	−0.0142	−0.7715	−0.0563
Interpretation[c]	C, T, C*T	D, D*A	A, D*A	C	T	D
	Multiple regression on principal components					
P value	0.0001	0.0001	0.0594	0.0265	0.0001	0.4445
Partial R^2 (Type II)	0.2906	0.2856	0.0299	0.0426	0.1548	0.0046
Parameter estimate	−3.6236	4.7554	1.9063	3.5466	−23.7497	14.9198
Standard error	0.5887	0.7794	0.9650	1.5040	5.2258	19.2048

[a] ln = The natural logarithmic function.
[b] Interaction terms are denoted by an asterisk between symbols.
[c] A = Standard age (years); D = Stand density (stem/ha); C = Distance (m) from the cavity-tree location to the midpoint of a stand divided by home range diameter; T = Distance (m) from the territorial focal point to the midpoint of a stand divided by home-range diameters.

effects on stand use. Principal Components 1, 4, and 5 can be interpreted as a localizing aspect of differential stand use, whereas Principal Components 2 and 3 are habitat quality aspects of differential stand use. Based on the proportion of variance explained by each principal component, the partial R^2s, and parameter estimates for each principal component, the localizing aspect accounts for the majority of variation in the differential stand use regression model, whereas the habitat quality aspect is less important (Table 3). A regression of the residuals from this model versus stand size is not significant ($P = 0.34$), thus indicating that none of the model variables interacts with stand size. A regression model with dbh in place of age was similar in all respects, but provided a slightly poorer fit ($R^2 = 0.79$).

The original variable form of the standardized regression of differential stand use (DSU) is:

$$\mathrm{DSU} = 0.0 + 12.34 \ln \mathrm{D} + 11.43 \ln \mathrm{A} - 4.13 \ln \mathrm{A} \ln \mathrm{D} - 6.90\,\mathrm{C} - 15.78\,\mathrm{T} + 15.14\,\mathrm{CT} \qquad \text{(Eq. 1)}$$

The regression equation for the intercept form of the original variables for differential stand use is:

$$\mathrm{DSU} = -91.37 + 15.84 \ln \mathrm{D} + 21.87 \ln \mathrm{A} - 1.78 \ln \mathrm{D} \ln \mathrm{A} - 29.63\,\mathrm{C} - 51.33\,\mathrm{T} + 39.47\,\mathrm{CT} \qquad \text{(Eq. 2)}$$

(See Table 3 for explanation of symbols.)

Differential stand use is not equally sensitive to the original variables in the regression model (Eq. 2). For a 1% increase from the mean of each variable, the changes in differential stand use for density, age, cavity tree location, and territorial effects are 0.0919, 0.1318, −0.0361, and −0.1735, respectively, corresponding to relative sensitivities (Smith 1970) of 53.0, 76.0, 20.0, and 100%. Thus, although the localizing effects are more variable than habitat quality (Table 2), and the regression model accounts for proportionally more of this greater variability (Table 3), the model is, overall, slightly more sensitive to habitat quality.

The relative sensitivity implications of the two localizing and two quality aspects of the regression model (Eq. 1) best can be evaluated graphically. Differential stand use depends simultaneously on the distance of the stand from the cavity trees and the focal point of territory activity (Fig. 2) and simultaneously on pine stand age and density (Fig. 3). For each figure, the zero or positive and negative differential stand use lines correspond to the regression line or parallel lines for observed stand use versus stand size.

Differential stand use is not equally sensitive to stand distance from the cavity trees and territorial focal point (Fig. 2). Based on a differential

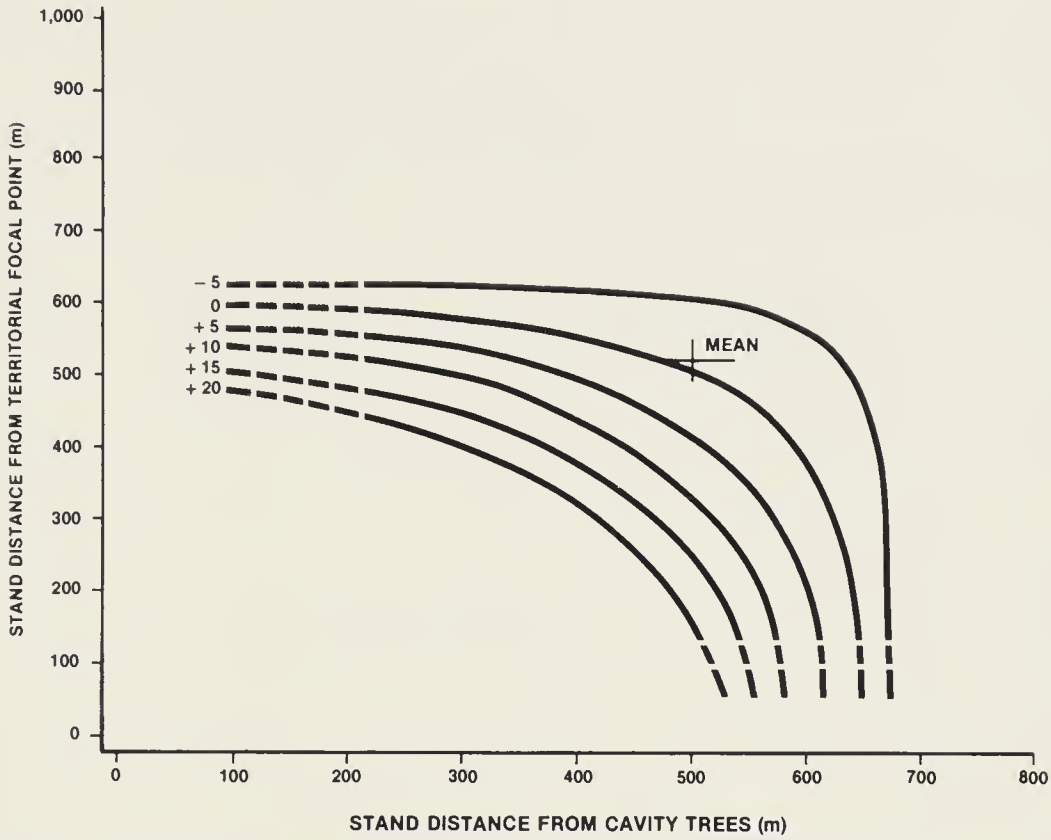

FIG. 2. Isoclines of differential stand use in relation to distance from the midpoint of a stand to the cavity trees and territorial focal point. Dashed line segments are beyond range of data.

stand use change from +5 to −5%, the changes in stand distance from the mean cavity tree location and mean territorial focal point are 315 and 645 m for cavity tree (81% change) and 432 and 599 m for territory (39% change). Thus, differential stand use is twice as sensitive to territorial focal point as it is to cavity tree location where the model can be expected to be most stable. For stands closer to the cavity trees, differential stand use is highly sensitive to territorial focal point. Conversely, for stands near the territorial focal point, differential stand use is more sensitive to cavity tree location. Differential stand use curves above −5% do not have the same form and are omitted from the figure.

Differential stand use is an inverse nonlinear function of pine stand age and density (Fig. 3). For a given age, differential stand use increases with density; for a given density, differential stand use increases with age. With respect to a given level of differential stand use, however, there is a wide range of combinations of pine stand ages and densities which are equivalent. For a change in differential stand use from +5 to −5%, the changes from the mean age and mean density are 166 and 89 stems ha for density (87% change) and 52 and 33 years for age (58% change). Thus, differential

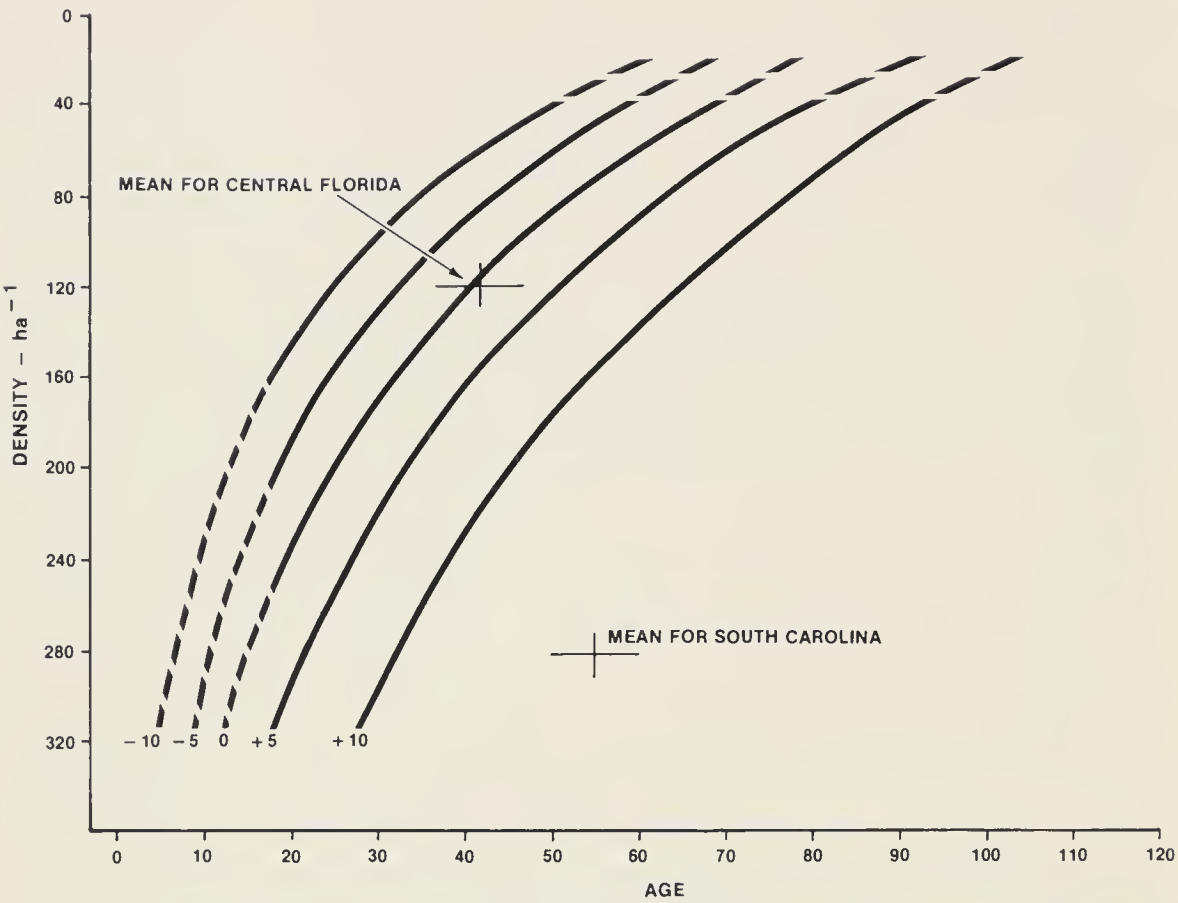

FIG. 3. Isoclines of differential stand use in relation to pine stand age and tree density. Note that the scale for density is inverted. Dashed line segments are beyond range of data.

stand use is 1.5 times more sensitive to age than it is to density. For denser stands, differential stand use is more sensitive to age. Conversely, for younger stands, differential stand use is slightly more sensitive to density.

DISCUSSION

Home range and territory use.—The central Florida site, although similar to habitats in more northerly latitudes, supports less dense stands of pines and smaller trees (DeLotelle et al. 1983). In addition to lower site productivity, pine stands have been subjected to logging activity over the last century. Moreover, study site habitats are similar to habitats containing Red-cockaded Woodpeckers elsewhere in central and south Florida (Nesbitt, pers. comm.).

Red-cockaded Woodpeckers in this central Florida site compensate for occupying resource-poor habitat in several ways. Average home range and territory sizes in central Florida are larger than average home range and territory sizes in South Carolina (Hooper et al. 1982) where habitat is better. Home range sizes in this study are closer to those reported by

Nesbitt et al. (1978, 1983) and Patterson and Robertson (1981) in peninsular Florida, who described home ranges of 58.4 to 213.2 ha. Available pine basal area in the current study site is similar to that available to woodpecker populations in south Florida (Nesbitt et al. 1983), which ranged from 265 to 485 m^2 ($\bar{x}$ = 7.0 m^2/ha). Central Florida group territories contained a mean pine basal area of 267.6 (2.3 m^2/ha), whereas Hooper et al. (1982) reported a mean pine basal area of 831.7 m^2 (11.8 m^2/ha) for 24 territories. Thus, territories and home ranges in central and south Florida are larger, but they contain less pine basal area than do those in South Carolina. Populations in north Florida (Porter 1984) appear intermediate, with home ranges somewhat smaller than central and south Florida and pine basal areas similar to those in South Carolina.

The larger territories and home ranges in central Florida incorporated 95% and 119% (i.e., 19% overlap) of available habitat, respectively, whereas the territories and home ranges in South Carolina incorporated only 64% and 75% of available habitat, respectively (Hooper, pers. comm.). This suggests that for the former, population density is near maximum. Under very similar average population densities (central Florida = 8.3; South Carolina = 8.8 groups/2000-m radius circle), central Florida groups require or use more habitat area for their territories compared to South Carolina groups and appear more constrained by population density in the poorer-quality habitat conditions found in central Florida.

As suggested by Wiens et al. (1985), habitat options for other bird species may become restricted at high population densities, resulting in occupancy of suboptimal territories. Conversely, individuals may use better habitats in areas with low population density (Wiens 1973). For Belted Kingfishers (*Megaceryle alcyon*) Davis (1982) found that habitat quality (i.e., the amount of preferred feeding habitat) had a significant inverse effect on both breeding and nonbreeding territory size, and that reduced population pressure resulted in individual kingfishers incorporating a greater resource base. The rate of incorporation of available habitat by the central Florida population of Red-cockaded Woodpeckers, which is 1.6 times that of the South Carolina population (Fig. 1), can be interpreted as a greater sensitivity of the central Florida population to poorer habitat conditions.

Two characteristics of foraging substrate selection can be interpreted as compensation effects for poor-quality habitat. Central Florida groups foraged on stems as small as 5 cm dbh (DeLotelle et al. 1983), whereas South Carolina groups were seldom observed on stems less than 13 cm dbh (Hooper and Lennartz 1981). More importantly, a larger proportion of foraging use occurred (21% use; 22% availability) on smaller size class stems (5–11 cm dbh) compared to the use of similar size classes (8% use;

55% availability) in South Carolina and north Florida (0.8% use; availability not reported) (Porter 1984). There are practical limits to this compensation, as woodpeckers were never observed to forage on pine stems <5 cm dbh, and those ≥10 cm dbh were preferred (DeLotelle et al. 1983). In addition, groups in central Florida made extensive seasonal use of cypress as an alternate foraging resource, whereas populations in northern Florida and South Carolina are seldom observed to use available hardwoods or cypress. During the fall of 1980, use of cypress was 20% (DeLotelle et al. 1983). Thus, in forests of substantially different densities and available tree sizes, foraging Red-cockaded Woodpeckers showed flexibility in their use of foraging habitats.

The higher frequency of observed extraterritorial foraging and group interactions can also be interpreted as an indication of resource-poor habitat. Myers et al. (1979) suggested that for Sanderlings (*Calidris alba*) it may be important for territorial residents to obtain part of their daily energy from sources away from their own territories. In our study, extraterritorial foraging and group interactions were 50% more common than in South Carolina (Hooper et al. 1982). Furthermore, in the current study groups averaged 277.1 m on extraterritorial trips, while the South Carolina groups averaged only 220.3 m.

Habitat use.—Nest- and roosting-site locations and territorial competition are factors influencing the use of habitat in many species. Defense behavior has been observed to influence territory use in other species (Eckhardt 1979, Myers et al. 1979). Territorial influences also affect Red-cockaded Woodpeckers in central Florida, which were observed to cross their territory in response to an intruding group. After such interactions, resident groups continued to forage in the area. In addition, the frequency of territorial interaction is greater in central Florida than South Carolina (Hooper et al. 1982). Thus, the relatively high sensitivity of stand use to territoriality reported here may be less important elsewhere. As inferred by Hooper (pers. comm.) and Seastedt and MacLean (1979), nest site location has an important influence on resource use. Although the effect of territoriality may be less pronounced in more optimal habitat, our results (Fig. 2) suggest that territoriality would remain more important than cavity tree location.

Despite the unbiased strong fit of the regression equation, the sensitivity analysis curves for cavity tree location and territorial focal point change form above −5% (Fig. 2). The change in form could result from behavior not accounted for by the model, or from measurement sources. The change in form may indicate a switch in foraging strategy due to distance effects as reported for the Gila Woodpecker (*Melanerpes uropygialis*) (Martindale 1983). When they were near roosting sites and territorial interaction sites,

Red-cockaded Woodpeckers were engaged in foraging activities, but they also performed other activities, such as cavity defense or scanning and listening for neighbors. At greater distances from these two sites, these nonforaging behavioral patterns were less apparent, and foraging was the primary activity. Seasonal changes in foraging patterns may also have influenced the results as reported by Conner (1981) for other woodpeckers. Marked seasonal changes in the foraging use of cypress were observed (DeLotelle et al. 1983), which could have influenced pine stand use. Alternatively, there are several possible measurement sources for the change in form. As is often the case in survey research, there is not a complete distribution of values for each variable with respect to all other variables. Clearly, there is less precision in the measurement of the territorial focal point compared to other parameters. Also, uncertainty exists in the placement of territory boundary segments based on use alone.

The sensitivity analysis shows stand age to be more important than stand density in determining stand use. Analysis of stand preference suggests that age or dbh and density influence stand use (Wood 1983; Porter 1984; Hooper, pers. comm.). Our sensitivity analysis quantifies the greater relative importance of age versus density over most of the range of age and density; however, there exists a range of combinations of ages and densities that are equivalent (Fig. 3). Stand densities in our study were not sufficiently high enough to have the inhibiting effect on stand use that occurs in north Florida (Porter 1984) and South Carolina (Hooper, pers. comm.). For moderately young stands, it is probable that there is an optimum range of densities. Whether age or dbh is more descriptive of differential stand use (or preference) is unknown.

A model of observed habitat use employing multivariate statistical procedures explains 93% of the variation in stand use for a population of Red-cockaded Woodpeckers in central Florida. In addition, sensitivity analyses (Smith 1970) provide a procedure for obtaining further interpretive insight (Wiens and Innis 1974) into the information content of complex regression models. In particular, our sensitivity analysis reveals that differential stand use is most sensitive to the effects of territorality followed by stand age, stand density, and cavity-tree location. This result quantifies suggestions that habitat quality influences stand use (Hooper, pers. comm.; Porter 1984), and indicates clearly that interpretation of stand use requires consideration of the influences of territoriality and the location of cavity trees.

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USE OF EVEN-AGED STANDS BY WINTER AND SPRING BIRD COMMUNITIES

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ABSTRACT.—I examined habitat use by winter and spring bird communities from 1981 to 1984 in 1-ha even-aged stands managed for Ruffed Grouse (*Bonasus umbellus*) in central Pennsylvania. Species richness was higher in edges than interiors of stands in both seasons. Edges of clearcut stands were avoided by winter birds but were used extensively by spring birds. In winter, the bird community seldom used the lower stratum near ground level (≤ 1 m), perhaps due to snow and ice cover. Both winter and spring avifauna foraged extensively on rough-barked overstory trees (e.g., *Quercus* and *Pinus*). Vertical strata use was more stereotypic in spring than in winter, whereas tree species use was more stereotypic in winter than in spring. Rough-barked overstory trees, snags, and slash should be retained in even-aged stands. *Received 12 July 1986, accepted 22 Sept. 1986.*

An understanding of habitat use by avifauna in forests altered by clearcutting is valuable information due to recent concern about the effects of forest fragmentation on avian population declines in eastern deciduous forests (e.g., Whitcomb et al. 1981). For example, species that are generalists in terms of habitat use may be better adapted and, hence, less sensitive to forest fragmentation resulting from even-aged management than those that are more specialized (Kroodsma 1984a, Franzreb 1985). In addition, habitat use by birds in even-aged stands may suggest how coexisting species partition resources in a modified environment. Interspecific partitioning may be achieved by differences in use of forest edge versus interior (Strelke and Dickson 1980, Kroodsma 1984a), vertical strata (Dickson and Noble 1978, Yahner 1982), or tree or shrub species (Franzreb 1978, Yahner 1982, Rice et al. 1984) and by differences in foraging behavior (Maurer and Whitmore 1981).

A Ruffed Grouse (*Bonasus umbellus*) habitat management study at the Barrens Grouse Management Study Area (BGMA) in central Pennsylvania has resulted in a mosaic of even-aged stands of aspen (*Populus* spp.) and mixed-oak (*Quercus* spp.) cover types via forest clearcutting (Yahner 1986). My objective was to examine habitat use by bird communities and individual species during winter and spring in even-aged stands at the BGMA.

STUDY AREA AND METHODS

I conducted the study at the BGMA, State Game Lands 176, Centre County, Pennsylvania. Approximately one-half (treated sector) of the BGMA is subdivided into contiguous, 4-ha

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blocks (N = 136) as part of a Ruffed Grouse habitat management study under the supervision of the Pennsylvania Game Commission. Sixty and 76 blocks are in aspen and mixed-oak cover type, respectively. Common overstory tree species include bigtooth aspen (*Populus grandidentata*), quaking aspen (*P. tremuloides*), and pitch pine (*Pinus rigida*) in aspen type, and white oak (*Quercus alba*), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), northern red oak (*Q. rubra*), and red maple (*Acer rubrum*) in mixed-oak type. Principal understory and shrub species are aspen, scrub oak (*Q. ilicifolia*), dwarf chinkapin oak (*Q. prinoides*), and black cherry (*Prunus serotina*) in aspen type; whereas *Quercus* spp. and red maple predominate in mixed-oak type. Aspen type generally is distributed within 400 m to each side of an unimproved dirt road that bisects the BGMA in a NE–SW direction; mixed-oak type is located >400 m from the road.

Each block is subdivided into four 1-ha stands (100 × 100 m). Using a clockwise cutting rotation of 20 and 40 years within aspen and mixed-oak blocks, respectively, five stands of distinct age and cover type (hereafter termed "habitats") were created. These include 1976–77 aspen and 1976–77 oak (western stand cut during winter 1976–77 in both aspen and mixed-oak blocks, respectively), 1980–81 aspen (northern stand cut during winter 1980–81 in aspen type only), and mature aspen and mature oak habitats (60-year-old stands in aspen and mixed-oak blocks, respectively). I selected three 1-ha stands in each of the five habitats for study. Stands chosen were representative of vegetative features and were >50 m from the unimproved and restricted access roads, frost pockets, and transmission-line corridors (Yahner 1986). Maximum distance among stands was 1 km.

I conducted 10 bird counts each winter (December–early March) and spring (April–June) from December 1981 to June 1984, making 30 counts per season during the 3-year period. Counts were made approximately once per week each year. I visited all stands on the same day (sunrise–10:30) and randomized the order of visits to individual stands for each count. Time spent (8–12 min) in each stand was similar in winter and spring. Birds seen or heard in each stand and 25 m into adjacent stands were noted along two 100-m transects spaced 50 m apart; birds flying above the canopy were not counted.

I assessed habitat use by noting the location of individual birds at initial sighting (Bradley 1985) in horizontal and vertical dimensions and in the type of tree species used. Ten horizontal zones were recognized, corresponding to edge and interior zones in the five habitats. An edge zone was the 25-m wide strip to each side of a boundary separating two stands of similar age and type. The area (ha) available per horizontal zone in each habitat was calculated.

I distinguished among four vertical strata: ground (ground level–1 m), lower midstory (1.1–6.0 m), upper midstory (6.1–12 m), and canopy (>12 m). The total volume (m^3) of vegetation available to birds was estimated by summing the products of the average height of vegetation per habitat and the total area of a given habitat (cf. Yahner 1982). Average height of vegetation in each habitat was based on 12, randomly selected, 0.04-ha circular plots per habitat (see details of vegetative sampling methods in Yahner and Grimm 1984).

I considered eight tree species: bigtooth-quaking aspen, pitch pine, white-chestnut oak, red-scarlet oak, scrub oak (*Q. ilicifolia* and *Q. prinoides* combined), black cherry, red maple, and slash (fallen log >1 m long and >3 cm in diameter). Snags and *Carya* spp. were not included in the analyses, thereby eliminating tree species that were uncommon and thus not readily available to the bird community (cf. Yahner 1982). I estimated the availability (no. stems/ha) of each tree species from the 12 circular plots per habitat; estimates for each tree species (excluding slash) were based on all woody stems >2.5 cm dbh and >1.5 m tall.

I compared observed versus expected numbers of sightings for all species combined and for individual common species (>30 total sightings per season) among horizontal zones, vertical strata, or tree species in both winter and spring using *G*-tests for goodness-of-fit and

independence (Sokal and Rohlf 1981). Analyses were not conducted if more than 20% of the expected sightings were less than five. In some cases, data were pooled from more than one level (e.g., mature aspen edge plus mature oak edge) to increase sample sizes. Although most birds were either singing or foraging, sightings were not analyzed on the basis of behavior (Yahner 1982).

Relationships among common bird species in habitat use were determined by *Q*-factor analysis (Dixon 1983). The observed number of sightings in 10 horizontal zones, 4 vertical strata, and 8 tree species represented 22 rows of the data matrix, and the 2 common species in winter and 17 common species in spring comprised the 19 columns (variables) of the matrix. A varimax (orthogonal) rotation was used; factors were extracted based on eigenvalues >1.0 (Rummel 1970).

I calculated horizontal (*HB*), vertical (*VB*), and tree species breadth (*SB*) for all species of birds combined and for individual common species in winter and spring. These indices were used to compare the relative degree of specialization of all species combined between winter and spring and among common species within a season (Yahner 1982, Franzreb 1985). I based each index on the equation: *HB, VB,* or $SB = 1 - 0.5\ \Sigma|p_i - q_i|$ where p_i is the proportion of observed sightings and q_i is the proportion of expected sightings in the *i*th horizontal zone, vertical stratum, or tree species, respectively (Feinsinger et al. 1981). Values of breadth indices ranged from 0 to 1, with 0 indicating maximum specialization. I derived a total habitat breadth for all species combined and for each common species in winter and spring by summing the three indices (maximum value of total habitat breadth = 3).

RESULTS AND DISCUSSION

Horizontal zone use.—I noted 206 sightings of individual birds from 13 species in winter and 2042 sightings from 69 species in spring. Regardless of habitat, I found that species richness was higher in edge than in interior zones in both winter and spring (Tables 1 and 2). Based on the total number of observed sightings per zone for all species combined, mature aspen interiors were preferred in winter and spring, whereas 1976–77 aspen edges and 1980–81 aspen habitat in general were avoided by winter birds. Thus, I view the youngest clearcut stands (1980–81 aspen habitat) as relatively unimportant to wintering avifauna (see also Yahner 1986). Horizontal breadth for all species combined in winter ($HB_w = 0.79$) (Table 1) and spring ($HB_s = 0.82$) (Table 2) was similar.

Black-capped Chickadees and Downy Woodpeckers (scientific names are in Tables 1 and 2) were the only common species in winter, and both species tended to use interiors of mature habitats more than expected (Table 1). Perhaps interiors of mature 1-ha stands afforded a better microclimate while foraging in winter compared to edges (Ranney et al. 1981, Morrison et al. 1986). Chickadees were generalists in use of horizontal zones ($HB_w = 0.73$) compared to Downy Woodpeckers ($HB_w = 0.66$).

I noted 17 common species in spring, and each established territories at the BGMA every year. The observed number of sightings per zone was significantly different from expected in 13 species (Table 2). HB_s was

TABLE 1

HORIZONTAL USE OF INTERIOR AND EDGE ZONES IN FIVE HABITATS AND HORIZONTAL BREADTH (HB_w) AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, IN WINTER 1981–84

	Habitat										
	Mature aspen		Mature oak		1976–77 aspen		1976–77 oak		1980–81 aspen		
	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	HB_w
Total area (ha)	1.46	5.40	3.72	3.29	1.01	4.08	0.92	2.92	1.10	4.08	
Species richness	4	8	8	9	3	6	3	8	0	2	
Total observed sightings (no./ha):											
All species[a]	15.8[b]	8.2	8.6	10.0	5.0	5.1[c]	5.4	8.2	0.0[c]	0.7[c]	0.79
Downy Woodpecker[a] (*Picoides pubescens*)	4.8[b]	1.9	3.5[b]	3.0	1.0	0.7	0.0	0.3	0.0	0.5[c]	0.66
Black-capped Chickadee[a] (*Parus atricapillus*)	8.9[b]	3.7	2.4	1.2[c]	0.0	2.9	2.1	3.8	0.0	0.7[c]	0.73

[a] Observed vs expected number of sightings was significantly different among zones in two or more habitats; G-test for goodness-of-fit.
[b] Observed number of sightings was significantly greater than expected in this zone compared to others combined; G-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.
[c] Observed number of sightings was significantly less than expected in this zone compared to others combined; G-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.

TABLE 2

HORIZONTAL USE OF INTERIOR AND EDGE ZONES IN FIVE HABITATS AND HORIZONTAL BREADTH (HB_s) AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, IN SPRING 1982–84

	Habitat										
	Mature aspen		Mature oak		1976–77 aspen		1976–77 oak		1980–81 aspen		
	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	HB_s
Species richness	37	55	40	42	20	32	12	26	11	21	
Total observed sightings (no./ha):											
All species[a]	104.1[b]	60.7[c]	42.7[c]	66.9	114.9[b]	112.0[b]	93.5[b]	88.7[b]	59.1	49.0[c]	0.82
Great Crested Flycatcher (*Myiarchus crinitus*)	2.1	3.0[b]	2.7[b]	0.9	0.0	0.3[c]	0.0	0.3	0.0	0.0	0.42
Blue Jay[a] (*Cyanocitta cristata*)	7.5[b]	2.8	5.9[b]	4.0	0.0	0.7[c]	2.2	0.7[c]	0.0	0.0	0.63
Black-capped Chickadee[a] (*Parus atricapillus*)	6.9	9.1[b]	1.3[c]	2.4[c]	10.9[b]	5.4[b]	2.2	1.4[c]	0.0	0.03[c]	0.57
Gray Catbird[a] (*Dumetella carolinensis*)	2.7[c]	2.8[c]	0.8[c]	1.2[c]	7.9	9.3[b]	20.7[b]	17.1[b]	3.6	1.5[c]	0.53
Red-eyed Vireo[a] (*Vireo olivaceus*)	4.8[b]	0.7	1.9[b]	4.0[b]	0.0	0.0[c]	0.0	0.0[c]	0.0	0.0[c]	0.46
Black-and-white Warbler[a] (*Mniotilta varia*)	9.6[b]	4.4[b]	3.2	5.2[b]	1.0	2.5	0.0	0.7[b]	0.0	0.0[c]	0.69
Golden-winged Warber (*Vermivora chrysoptera*)	2.7	1.3	0.0[c]	1.5	7.9[b]	1.5	0.0	4.1[b]	0.9	1.2	0.62
Nashville Warbler (*V. ruficapilla*)	0.7	4.1[b]	0.8	0.6	12.9[b]	0.0[c]	0.0	1.0	0.9	0.0	0.47
Chestnut-sided Warbler[a] (*Dendroica pensylvanica*)	0.0[c]	1.3[c]	0.0[c]	0.6[c]	6.9[b]	9.1[b]	5.4	5.8[b]	0.9	0.7[c]	0.45

Table 2 Continued

Horizontal Use of Interior and Edge Zones in Five Habitats and Horizontal Breadth (HB_s) at the Barrens Grouse Habitat Management Study Area, Centre County, Pennsylvania, in Spring 1982–84

	Habitat										
	Mature aspen		Mature oak		1976–77 aspen		1976–77 oak		1980–81 aspen		
	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	HB_s
Ovenbird[a] (*Seiurus aurocapillus*)	16.4[b]	2.2	7.5[b]	6.7[b]	0.0	0.7[c]	1.1	3.6[c]	0.0	0.0[c]	0.55
Common Yellowthroat[a] (*Geothlypis trichas*)	1.4[c]	1.5[c]	1.6[c]	0.3[c]	14.9[b]	19.4[b]	32.6[c]	15.4[b]	7.3	8.3	0.55
Brown-headed Cowbird[a] (*Molothrus ater*)	3.4	3.5[b]	0.3[c]	5.2[b]	0.0	1.5	1.1	0.0[b]	0.0	0.0[c]	0.56
Indigo Bunting[a] (*Passerina cyanea*)	0.0	3.9[b]	0.0[c]	10.9[b]	0.0	0.0[c]	2.2	3.8	0.0	1.0	0.58
American Goldfinch[a] (*Carduelis tristis*)	0.0	1.7	0.0	1.8	3.0	2.9[b]	0.0	0.0	3.6	0.5	0.66
Rufous-sided Towhee[a] (*Pipilo erythrophthalmus*)	14.4	11.5	2.2[c]	3.6[c]	15.8	29.4[b]	16.3	26.7[b]	11.8	12.3	0.71
Chipping Sparrow (*Spizella passerina*)	2.7	18.7[b]	0.0	0.0	0.0	0.2	0.0	0.0	0.0	1.2	0.38
Field Sparrow[a] (*S. pusilla*)	2.1[c]	1.7[c]	0.3[c]	0.6[b]	19.8[b]	18.3[b]	7.6	4.5[c]	24.5[b]	18.9[b]	0.51

[a] Observed vs expected number of sightings was significantly ($P < 0.01$) different among zones in two or more habitats; G-test for goodness-of-fit.
[b] Observed number of sightings was significantly greater than expected in this zone compared to others combined; G-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.
[c] Observed number of sightings was significantly less than expected in this zone compared to others combined; G-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.

lowest in Chipping Sparrows (0.38) and highest in Rufous-sided Towhees (0.71).

Ovenbirds and Blue Jays occurred more often than expected in mature interiors, whereas Red-eyed Vireos and Black-and-white Warblers typically used both zones in mature habitats more than expected. Strelke and Dickson (1980) generally found these 4 species associated with mature woods. However, territories of Ovenbirds and Red-eyed Vireos are usually away from edges (>25 m), and those of Blue Jays and Black-and-white Warblers tend to be near edges (Chasko and Gates 1982, Kroodsma 1984a).

Indigo Buntings and Brown-headed Cowbirds preferred edges of mature habitats in my study (Table 2) and in others (Yahner and Howell 1975, Brittingham and Temple 1983). Gray Catbirds, Chestnut-sided Warblers, and Rufous-sided Towhees, which are species characteristic of brushy vegetation or edges in disturbed habitats (Anderson et al. 1977, Chasko and Gates 1982, Niemi and Hanowski 1984), typically occurred in edges of 1976–77 habitats. Catbirds also were common in interiors of the relatively isolated 1976–77 oak habitat. Greater use of mature-clearcut habitat interfaces by avian species at the BGMA in spring may be due to greater diversity and abundance of food resources in edges compared to interiors, preference for nest sites along habitat discontinuities, and presence of conspicuous and readily accessible song perches (Strelke and Dickson 1980, Ranney et al. 1981, Kroodsma 1984b).

Two species were characteristic of both zones in clearcut stands: Common Yellowthroats in 1976–77 habitats and Field Sparrows in 1980–81 aspen habitat (Table 2). Perhaps an edge effect at the BGMA for these edge specialists (e.g., Johnston 1947) was minimal because of abundant brushy vegetation throughout clearcut stands (see Kroodsma 1984b).

Vertical strata use.—In winter and spring, species richness was highest in the lower midstory stratum (Tables 3 and 4). The ground stratum was used disproportionately more than expected in both seasons, based on the total number of observed sightings per stratum for all species combined. Moreover, I found that the ground stratum was used much more by spring birds than winter birds ($G = 18.5$, df = 1, $P < 0.001$), whereas the upper midstory stratum was used more in winter than in spring ($G = 12.4$, df = 1, $P < 0.001$). A lower vertical habitat breadth by all species combined in spring ($VB_s = 0.69$) (Table 4) compared to winter ($VB_w = 0.80$) (Table 3) may be attributed mainly to higher use of the ground stratum by spring avifauna. I believe that the presence of snow and ice cover in winter at the BGMA likely reduced use of the ground stratum. In contrast, birds of Louisiana bottomland forests foraged more often in lower strata during winter than in spring (Dickson and Noble 1978), perhaps because of relatively snow-free winters at those lower latitudes.

TABLE 3

VERTICAL USE OF FOUR STRATA AND VERTICAL BREADTH (VB_w) AT THE BARRENS GROUSE MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, IN WINTER 1981–84

	Stratum				
	Ground	Lower midstory	Upper midstory	Canopy	VB_w
Total volume of vegetation (m^3)	281,400	1,045,900	838,200	698,500	
Species richness	8	11	7	5	
Total observed sightings (no./10,000 m^3):					
All species[a]	1.71[b]	0.76	0.44[c]	0.42[c]	0.80
Downy Woodpecker[a]	0.00[c]	0.21	0.17	0.13	0.86
Black-capped Chickadee[a]	0.64[b]	0.36[b]	0.13[c]	0.14[c]	0.74

[a] Observed vs expected number of sightings was significantly different among the four strata; G-test for goodness-of-fit, $G \geq 9.3$, df = 3, $P < 0.05$.
[b] Observed number of sightings was significantly greater than expected in this stratum compared to others combined; G-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.
[c] Observed number of sightings was significantly less than expected in this stratum compared to others combined; $G \geq 3.8$, df = 1, $P < 0.05$.

TABLE 4

VERTICAL HABITAT USE OF FOUR STRATA AND VERTICAL BREADTH (VB_s) AT THE BARRENS GROUSE MANAGEMENT AREA, CENTRE COUNTY, PENNSYLVANIA, IN SPRING 1982–84

	Stratum				
	Ground	Lower midstory	Upper midstory	Canopy	VB_s
Species richness	32	50	40	36	
Total observed sightings (no./10,000 m³):					
All species[a]	22.0[b]	5.4	1.8[c]	2.7[c]	0.69
Great Crested Flycatcher[a]	0.0	0.0	0.2[b]	0.1	0.63
Blue Jay[a]	0.0	0.1[c]	0.2[b]	0.1	0.76
Black-capped Chickadee[a]	0.6[b]	0.4[b]	0.1[c]	0.1[c]	0.69
Gray Catbird[a]	1.0[b]	0.6[b]	0.0[c]	0.0[c]	0.50
Red-eyed Vireo[a]	0.0	0.1	0.1	0.1[b]	0.75
Black-and-white Warbler[a]	0.1	0.3[b]	0.1	0.1[c]	0.70
Golden-winged Warbler[a]	0.4	0.4[b]	0.0[c]	0.0[c]	0.71
Nashville Warbler	0.1	0.2[b]	0.0	0.0	0.77
Chestnut-sided Warbler[a]	0.4[b]	0.3[b]	0.0[c]	0.0[c]	0.49
Ovenbird	0.8[b]	0.1	0.0[c]	0.0[c]	0.46
Common Yellowthroat[a]	3.8[b]	0.6	0.0[c]	0.0[c]	0.48
Brown-headed Cowbird[a]	0.0[c]	0.0[c]	0.01[c]	0.6[b]	0.35
Indigo Bunting[a]	0.1	0.3[b]	0.1	0.1[c]	0.71
American Goldfinch[a]	0.3	0.1	0.1	0.1	0.79
Rufous-sided Towhee[a]	7.5[b]	0.7[c]	0.1[c]	0.1[c]	0.38
Chipping Sparrow[a]	0.1	0.0[c]	0.1	0.3[b]	0.67
Field Sparrow	5.4[b]	0.3[c]	0.0[c]	0.0[c]	0.29

[a] Observed vs expected number of sightings was significantly different among the four strata; G-test for goodness-of-fit, $G \geq 9.3$, df = 3, $P < 0.05$.

[b] Observed number of sightings was significantly greater than expected in this stratum compared to others combined; G-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.

[c] Observed number of sightings was significantly less than expected in this stratum compared to others combined; $G \geq 3.8$, df = 1, $P < 0.05$.

I observed Black-capped Chickadees more often than expected in the two lower strata, but Downy Woodpeckers avoided the ground stratum in winter (Table 3). Relative values of VB_w suggest that Downy Woodpeckers were less stereotypic in vertical use of space than Black-capped Chickadees during winter.

In spring, Ovenbirds, Common Yellowthroats, Rufous-sided Towhees, and Field Sparrows were characteristic of the ground stratum; Black-capped Chickadees, Gray Catbirds, and Chestnut-sided Warblers restricted most activity to the two lower strata; Great Crested Flycatchers and Blue Jays preferred the upper midstory stratum; and Red-eyed Vireos, Brown-headed Cowbirds, and Chipping Sparrows tended to occur in the canopy stratum (Table 4). Species with relatively low VB_s (<0.40) re-

stricted most vertical movements to one stratum (e.g., Field Sparrow, Brown-headed Cowbird) (Table 4). Seven species were flexible (VB_s > 0.70) in stratum use during spring.

Vertical strata use by individual species in my study was similar to that reported by others (e.g., Dickson and Noble 1978, Yahner 1982), with the exception that Black-capped Chickadees, Red-eyed Vireos, and Chipping Sparrows appeared to alter their vertical location in response to a modified environment. For example, in manmade farmstead shelterbelts, I typically noted Chipping Sparrows on the ground rather than in vegetation of different heights (Yahner 1982). Mowing practices within and adjacent to shelterbelts often result in well-manicured lawns that are used extensively for foraging Chipping Sparrows (Yahner 1983). In a forest with modified vegetative structure due to clearcutting (about 20-years-old), Maurer and Whitmore (1981) generally observed Red-eyed Vireos foraging only about 10 m above ground.

Tree species use.—Species richness and the total number of sightings for all species combined were higher in white-chestnut oak, red-scarlet oak, bigtooth-quaking aspen, and pitch pine than in other species of trees (Table 5). In addition, slash was used more often than expected in spring, but avoided in winter; however, use of tree species by all species combined varied with season (G = 92.6, df = 7, P < 0.001). For instance, pitch pine, white-chestnut oak, red-scarlet oak, and black cherry were used disproportionately more by birds in winter than in spring (all G's > 4.0, df = 1, P < 0.05). Conversely, scrub oak, red maple, and slash were used more often by the spring bird community (all Gs > 9.3, df = 1, P < 0.01). Tree species breadth (SB) for the avian community in spring (0.39) was higher than in winter (0.16), indicating greater flexibility in choice of tree species by spring birds.

Downy Woodpeckers and Black-capped Chickadees in winter and seven common species in spring occurred more often than expected in white-chestnut oak, red-scarlet oak, bigtooth-quaking aspen, and pitch pine (Table 5). In contrast, I found Gray Catbirds, Common Yellowthroats, Rufous-sided Towhees, and Field Sparrows frequently foraging in slash. SB_w was 0.26 and 0.09 for Black-capped Chickadees and Downy Woodpeckers, respectively; SB_w ranged from 0.04 for Brown-headed Cowbirds to 0.65 for Common Yellowthroats.

Winter avifauna, in particular, presumably depended on overstory trees with rough or flaky bark (e.g., *Quercus, Pinus*) because of greater surface area there relative to smooth-barked trees. Rough-barked trees, with abundant crevices, provide a greater abundance of arthropods for foraging birds (Brawn et al. 1982, Morrison et al. 1985). Thus, rough-barked overstory trees, combined with slash and snags, are important features that

TABLE 5

TREE SPECIES USE AND BREADTH IN WINTER (SB_w) AND SPRING (SB_s) AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, 1981–84

	Tree species								
	Bigtooth-quaking aspen	Pitch pine	White-chestnut oak	Red-scarlet oak	Scrub oak	Black cherry	Red maple	Slash	*SB*
No. stems/ha	6847	97	310	148	347,500	39,100	58,996	3040	
Winter:									
Species richness	8	6	10	6	2	3	4	0	
Total observed sightings (no./1000 stems):									
All species[a]	7.3[b]	340.2[b]	222.6[b]	168.9[b]	0.1[c]	0.1[c]	0.1[c]	0.0[c]	0.16
Downy Woodpecker[a]	1.8[b]	92.8[b]	67.7[b]	67.6[b]	0.0[c]	0.1[c]	0.0[c]	0.0	0.09
Black-capped Chickadee[a]	3.8[b]	144.3[b]	58.1[b]	33.8[b]	0.1[c]	0.0[c]	0.1[c]	0.0	0.26
Spring:									
Species richness	42	27	40	27	17	20	23	7	
Total observed sightings (no./1000 stems):									
All species[d]	38.6[e]	1206.2[e]	561.3[e]	421.2[e]	0.5[f]	2.6	2.1	17.1[e]	0.39
Great Crested Flycatcher	0.6[e]	51.6[e]	12.9[e]	13.5[e]	0.0[f]	0.0	0.0	0.0	0.13
Blue Jay	0.7[e]	51.6[e]	48.4[e]	94.6[e]	0.0[f]	0.0	0.0	0.0[f]	0.09
Black-capped Chickadee[d]	3.9[e]	123.7[e]	38.7[e]	0.0	0.01[f]	0.1	0.1	0.0[f]	0.36
Gray Catbird[d]	2.5[e]	0.0	38.7[e]	0.0	0.0[f]	0.2	0.4[e]	0.0[e]	0.36
Red-eyed Vireo	0.2	0.0	22.6[e]	6.8	0.0	0.0	0.1[e]	0.0	0.33
Black-and-white Warbler[d]	1.5[e]	103.1[e]	51.6[e]	0.5[e]	0.0[f]	0.0	0.1	0.0	0.11
Golden-winged Warbler[d]	3.5[e]	0.0	3.2	13.5[e]	0.0[f]	0.3[e]	0.2	0.0	0.37
Nashville Warbler	1.5[e]	30.9[e]	0.0	0.0	0.0[f]	0.1	0.0	0.0	0.39
Chestnut-sided Warbler[d]	68.5[e]	61.9[e]	9.7[e]	6.8[e]	0.0[f]	0.2	0.2	0.3	0.39

Table 5 Continued

Tree Species Use and Breadth in Winter (SB_w) and Spring (SB_s) at the Barrens Grouse Habitat Management Study Area, Centre County, Pennsylvania, 1981–84

	Tree species								
	Bigtooth-quaking aspen	Pitch pine	White-chestnut oak	Red-scarlet oak	Scrub oak	Black cherry	Red maple	Slash	*SB*
Ovenbird	0.4[e]	20.6[e]	3.2	0.0	0.0	0.0	0.1	0.0	0.24
Common Yellowthroat[d]	3.8[e]	10.3	19.4[e]	0.0	0.2[f]	0.4	0.5[e]	3.0[e]	0.65
Brown-headed Cowbird[d]	1.9[e]	216.5[e]	19.4[e]	67.6[e]	0.0[f]	0.0	0.0[f]	0.0	0.04
Indigo Bunting[d]	2.2[e]	82.5[e]	12.9[e]	6.8[e]	0.0[f]	0.4[e]	0.1	0.0	0.25
American Goldfinch	1.6[e]	0.0	0.0	6.8[e]	0.0[f]	0.2[e]	0.0	0.0	0.24
Rufous-sided Towhee[d]	4.8[e]	61.9[e]	32.3[e]	0.0	0.0[f]	0.2	0.0[f]	5.3[e]	0.36
Chipping Sparrow	0.6[e]	175.3[e]	0.0	0.0	0.0	0.0	0.0	0.0	0.14
Field Sparrow[d]	1.3[e]	0.0	3.2	13.5[e]	0.1[f]	0.3	0.1	6.6[e]	0.61

[a] Observed vs expected number of sightings was significantly different among bigtooth-quaking aspen, pitch pine, white-chestnut oak, red-scarlet oak, and scrub oak; G-test for goodness-of-fit, $G \geq 9.5$, df = 4, $P < 0.05$.

[b] Observed number of sightings was significantly greater than expected in this tree species compared to others combined; $G \geq 3.8$, df = 1, $P < 0.05$.

[c] Observed number of sightings was significantly less than expected in this tree species compared to others combined; $G \geq 3.8$, df = 1, $P < 0.05$.

[d] Observed vs expected number of sightings was significantly different among three or more tree species; G-test for goodness-of-fit, $G \geq 3.8$, df = 2–7, $P < 0.05$.

[e] Observed number of sightings was significantly greater than expected in this tree species compared to others combined; G-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.

[f] Observed number of sightings was significantly less than expected in this tree species compared to others combined; G-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.

TABLE 6

HABITAT RELATIONSHIPS AMONG BIRD SPECIES BASED ON THE NUMBER OF OBSERVED SIGHTINGS IN 10 HORIZONTAL ZONES, 4 VERTICAL STRATA, AND 8 TREE SPECIES DURING WINTER AND SPRING AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, 1981–84

	Factor[a]			
	I	II	III	IV
Winter:				
Downy Woodpecker	0.45	0.83	−0.11	0.15
Black-capped Chickadee	0.73	0.37	0.42	0.20
Spring:				
Great Crested Flycatcher	0.06	0.69	−0.08	0.53
Blue Jay	−0.07	0.88	−0.13	0.25
Black-capped Chickadee	0.81	0.21	0.34	0.28
Gray Catbird	0.77	0.10	0.27	−0.41
Red-eyed Vireo	−0.03	0.81	−0.14	−0.01
Black-and-white Warbler	0.70	0.63	0.05	0.09
Golden-winged Warbler	0.89	−0.15	0.10	−0.15
Nashville Warbler	0.90	0.02	0.17	0.12
Chestnut-sided Warbler	0.84	−0.07	0.27	−0.25
Ovenbird	0.22	0.32	0.74	−0.07
Common Yellowthroat	0.35	−0.31	0.81	−0.26
Brown-headed Cowbird	−0.03	0.25	−0.17	0.78
Indigo Bunting	0.83	0.24	−0.14	0.10
American Goldfinch	0.69	−0.09	0.30	0.27
Rufous-sided Towhee	0.29	−0.25	0.89	0.00
Chipping Sparrow	0.11	0.12	−0.04	0.92
Field Sparrow	0.02	−0.43	0.84	−0.13
% variation explained	39.1	27.0	9.3	7.7

[a] A factor loading >0.50 is considered important to a given factor.

should be maintained in even-aged stands (Brawn et al. 1982, Morrison et al. 1985, Yahner 1986).

Habitat relationships among bird species.—Four factors extracted by factor analysis accounted for 83.1% of the total variance (Table 6). Factor I, termed "lower midstory—aspen," associated eight species that extensively used the 1.1- to 6-m stratum and aspen in their daily activities (factor loadings >. 0.50). Factor II was an "upper midstory—oak" factor because it included four species noted often in the 6.1- to 12-m stratum and in white-chestnut oak. Species exhibiting high factor loadings on the third factor, "ground stratum," were those spending considerable time in the lowest stratum. The last factor, labeled "canopy—pitch pine," grouped species that typically occurred at heights >12 m and in pitch pine. Thus,

although some avian species preferred certain horizontal zones over others (Tables 1 and 2), species were associated instead by habitat use of vertical strata and tree species. Similarly in farmstead shelterbelts, I found that coexisting avifauna also were clustered into several groups based on their use of specific vertical strata and tree species (Yahner 1982). Therefore, I propose that habitat segregation among species may be more effectively achieved in a localized area by differential use of vertical heights and tree species rather than by differential use of forest interiors and edges (cf. Paszkowski 1984).

Concluding remarks.—For all species combined, a lower habitat breadth in winter compared to spring suggests that the spring avifauna was relatively less affected by habitat fragmentation created by current clearcutting at the BGMA; however, seasonal differences in total habitat breadth was principally due to stereotypic use of tree species in winter (e.g., preference for rough-barked trees).

High total habitat breadth (>1.5) for Black-capped Chickadees in both winter and spring, Downy Woodpeckers in winter, and Red-eyed Vireos, Golden-winged Warblers, Nashville Warblers, Common Yellowthroats, and Indigo Buntings in spring may indicate that these species are less affected by the current cutting cycle compared with other species. Although additional clear-cutting may provide suitable habitat conditions for species adapted to brushy or edge habitats, I suspect that it likely will reduce the abundance and distribution of species associated with the "upper midstory—oak" and "canopy—pitch pine" factors in my study. Furthermore, additional cutting may increase nest predation and parasitism due to increased edge (Brittingham and Temple 1983).

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DIET AND FORAGING BEHAVIOR OF RING-BILLED GULLS BREEDING AT DOG LAKE, MANITOBA

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ABSTRACT.—Ring-billed Gulls (*Larus delawarensis*) breeding at Dog Lake, Manitoba, were almost exclusively terrestrially based in their foraging efforts. Major food items in late May to early June were earthworms and grain that were obtained by foraging behind farm cultivating implements. Insects increased in importance as the season progressed, particularly for female gulls. Gulls obtained insects by foraging along lakeshore ridges (mayflies) or behind haying implements (grasshoppers). Males obtained birds and mice in the latter part of the season by foraging behind haying implements. Chick diet (from late June to late July) closely paralleled that of adults. *Received 26 May 1986, accepted 19 Dec. 1986.*

Abundant food and the creation of new nesting habitat appear to be the main factors responsible for local population increases of Ring-billed Gulls (*Larus delawarensis*) across North America. Introduction of the alewife (*Alosa pseudoharengus*) into the Great Lakes, widespread intensification of agricultural activities, and the expansion of town and city garbage dumps have had positive effects upon food supplies (Ludwig 1974, Conover 1983); man-made reservoirs have permitted colonization into areas formerly unsuitable for breeding (Conover 1983).

Ring-billed Gull populations in Manitoba are considered to be increasing (Koonz and Rakowski 1985). Here I document foraging areas of a Manitoba population throughout the breeding season, determine food items taken, and relate these findings to other accounts of gull food habits.

MATERIALS AND METHODS

Study area.—The study area (approximately 6362 km^2) around Dog Lake, Manitoba (51°01′N, 98°29′W), contained three major Ring-billed Gull colonies with an estimated total of 3500 breeding pairs. Dominant vegetation in the area includes poplar (*Populus* spp.), spruce (mostly *Picea glauca*), bur oak (*Quercus macrocarpa*), and willow (*Salix* spp.) in the higher areas, and meadow grasses and sedges (*Carex* spp.) in the low areas. Less than half of the available land is used for agricultural crops, with most of the remainder used for grazing cattle. Of the total area in crop production, about 40% is sown to cereal crops, 40% tame hay, and 20% to oil seeds (Manitoba, Dept. Agric., unpubl. data).

Foraging habitat.—To assess the relative importance of different feeding sites to Ring-billed Gulls, I partitioned the foraging area into two halves (north and south). I drove through each half for one full day out to the maximum foraging radius (from previous observations I had determined this to be about 45 km; see also Baird 1976), and included as much lake area as could be observed from the shoreline. Each 2-day cycle (north and

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TABLE 1

NUMBER OF SITE-DAYS[a] RING-BILLED GULLS FORAGED IN VARIOUS HABITATS NEAR DOG LAKE, MANITOBA, AND THE MAXIMUM DAILY NUMBER AT FOUR MAJOR DUMPS, 1983 AND 1984[b]

Habitat	13–16 May	1–15 June	16–30 June	1–15 July	13–16 July
Agricultural land					
Pastures	31	21	4	0	0
Cultivated land[c]	6	42	11	6	1
Hayland[d]	0	3	14	31	12
Marsh, ridge	0	0	5	25	17
Dumps					
Ashern	182	165	50	60	27
Vogar	30	4	40	11	0
Dog Creek	110	33	45	6	5
Narrows	65	67	0	0	58

[a] A site-day is defined as the presence of gulls at a site on a given day without regard to number of gulls.

[b] χ^2 tests comparing frequencies of habitats used for successive time periods: $\chi^2 = 23.6$, df = 1, $P < 0.001$ (late May vs early June); $\chi^2 = 35.1$, df = 2, $P < 0.001$ (early vs late June); $\chi^2 = 16.3$, df = 2, $P < 0.001$ (late June vs early July); $\chi^2 = 1.6$, df = 1, $P > 0.10$ (early July vs late July); $\chi^2 = 217.2$, df = 12, $P < 0.001$ (all months combined). Note that in most cases cell frequencies were combined until <20% of cells had expected values <5. χ^2 statistics for comparison of late May vs early June and early July vs late July periods are corrected for continuity (Siegel 1956).

[c] Discing and seeding implements usually present.

[d] Cutting and bailing implements always present.

south) was repeated every 4–5 days. Upon encountering gulls at a site I recorded habitat type, number of birds, and food types taken. The latter was determined by direct observation.

Diet.—I collected 48 birds in 1984 from flocks in each habitat type, except for beach ridges, as birds foraging there were too wary to permit collection. In addition, 13 gulls that were flying towards the colonies were collected from four compass points (N,N = 3; S,N = 3; E,N = 3; W,N = 4) along the shore of Dog Lake. Collections were made from 4 May to 15 July, but only 2 birds were collected during the last half of June, when heavy rainfall and thunderstorm activity precluded any cultivating or harvesting activities for 9 out of 15 days. Collected birds were sexed by internal examination.

I also collected regurgitations from 13 chicks (in different parts of the colony) that ranged in age from 7 to 20 days. These regurgitations, as well as prey types recovered from the proventriculus and gizzard of collected adults, were preserved in 10% formalin and later identified.

RESULTS

Foraging habitat.—In late May and early June, all gulls were observed foraging on agricultural land, either behind tilling implements (where the principal food was worms and grain), or in pastures, where worms were available (Table 1). As the season progressed (late June onwards), the proportion of gulls on tilled land declined. From late June through the end of the season, marsh and ridge use increased, presumably in response

to emergence of aquatic insects. These insects were usually consumed from the ground, although an occasional gull was observed hawking above the marsh or ridge. Similarly, haying operations began at this time, and gulls fed on prey uncovered or injured by these implements (Table 1).

There was a significant tendency for pastures to be used during and within 3 days of rainfall (85% use during or within 3 days of rainfall vs 10% use at other times; $\chi^2 = 30.3$, df = 1, $P < 0.0001$). On the three occasions when pastures were used without rainfall, flock sizes were small (12–30 birds), and all birds were loafing at the time of observation. In both years, the use of pastures stopped in the latter part of June (Table 1).

On farmland, there were usually either many or no gulls present (mean flock size 107.5 ± 114.0, N = 207). In contrast, a few gulls were almost always observed at each refuse dump (mean flock size 31.3 ± 40.7, N = 50). Peak dump use occurred in May and declined through June and July (Table 1).

Diet.—In late May to early June, earthworms were the dominant prey by volume for those birds on pastures or land under cultivation (Table 2).

The two birds collected in late June returning to the colony had been feeding on insects (95% of the volume was exclusively mayflies). In July, samples taken from returning birds consisted predominantly of Orthopterans (grasshoppers) (Table 2).

From late May to early June, earthworms, insects, and grain were common in the diet of both sexes collected while foraging on pastures or cultivated land (frequencies for males: 67, 83, and 75%, respectively, N = 12; females: 79, 71, and 57%, respectively, N = 14; $\chi^2 = 0.462$, df = 2, $P > 0.05$). Though females averaged a greater volume of earthworms than did males (73 vs 47%), with males consuming larger amounts of grain (46 vs 20%), differences were not significant between sexes (Mann-Whitney *U*-test, $P > 0.05$, both food items tested separately). Insects comprised the remainder of the diet of both sexes.

There was no significant difference in the frequencies of prey taken for the combined July diets ($\chi^2 = 5.582$, df = 2, $P > 0.05$) (Table 3). Overall, males consumed greater volumes of birds and mammals than did females. Insects comprised the bulk of the female diet (Table 3).

Chick regurgitant reflected adult diets throughout the rearing period, which lasted from mid-June to the end of July. In the latter part of June, samples from 3 chicks had volumes of 76% insects and 24% grain. In July, chick regurgitant contained only insects (N = 10 chicks).

DISCUSSION

Foraging habitat.—The distribution of foraging gulls observed in this study indicates a pattern closely tied to agriculture. Despite widespread

TABLE 2

DIGESTIVE TRACT CONTENTS OF RING-BILLED GULLS COLLECTED AT FORAGING SITES OR RETURNING TO THE COLONY IN 1984

Food item	Foraging				Flying back to colony	
	16 May–15 June		1–31 July		1–31 July	
	Frequency (%)[a]	Volume (ml) (%)[b]	Frequency (%)	Volume (ml) (%)	Frequency (%)	Volume (ml) (%)
N	26		22		11	
Earthworms[c]	19 (73)	234.5 (61)	0	0	0	0
Birds (*Passerculus sandwichensis*)	0	0	3 (14)	62.5 (9)	2 (18)	54.8 (21)
Mammals (*Microtus* spp.)	0	0	13 (59)	487.8 (71)	2 (18)	28.3 (11)
Fish[d]	0	0	4 (18)	43.7 (7)	2 (18)	0.9 (1)
Grain	17 (54)	123.0 (32)	1 (5)	5.6 (1)	3 (27)	7.8 (3)
Frogs (*Rana pipiens*)	0	0	3 (14)	13.6 (2)	0	0
Insects	20 (77)	15.4 (4)	17 (77)	64.7 (9)	10 (91)	162.4 (62)
Adult Diptera	1 (5)	2.5 (16)	0	0	1 (10)	21.0 (13)
Orthoptera	0	0	5 (29)	49.2 (76)	7 (70)	133.6 (82)
Larvae	6 (30)	9.7 (63)	0	0	0	0
Other[e]	17 (85)	3.3 (21)	13 (76)	15.5 (24)	8 (80)	7.8 (5)
Debris[f]	6 (23)	11.5 (3)	4 (18)	6.8 (1)	3 (27)	7.8 (3)

[a] Percent of samples. Note that frequencies of insect groups are relative to the total insect sample.
[b] Percent of combined volumes. Volume percentages of insect groups are relative to total insect volume.
[c] Mostly Lumbricidae.
[d] One sample contained Perch (*Perca flavescens*). Four had Fat-head Minnows (*Pimapheles promelas*).
[e] Includes Coleoptera, Homoptera, Odonata, Ephemeroptera, Geophilomorpha, and unidentified insect parts.
[f] Soil particles, gravel.

TABLE 3

FREQUENCY AND VOLUME OF FOOD ITEMS FOR MALE AND FEMALE RING-BILLED GULLS COLLECTED IN JULY 1984

	Foraging				Flying back to colony			
	Male		Female		Male		Female	
Food items	Frequency (%)[a]	Volume (ml) (%)[b]	Frequency (%)	Volume (ml) (%)	Frequency (%)	Volume (ml) (%)	Frequency (%)	Volume (ml) (%)
N	18		4		4		7	
Birds	3 (17)	62.5 (10)	0	0	2 (50)	54.8 (59)	0	0
Mammals	12 (67)	487.3 (78)	1 (25)	0.5 (1)	1 (25)	28.3 (30)	1 (14)	trace
Fish	3 (17)	43.7 (7)	0	0	1 (25)	0.9 (1)	1 (14)	trace
Insects	13 (72)	12.5 (2)	4 (100)	52.2 (97)	3 (75)	5.5 (6)	7 (100)	156.9 (93)
Orthoptera	3 (23)	1.8 (14)	2 (50)	47.4 (91)	2 (67)	5.4 (98)	5 (71)	128.2 (82)
Other[c]	11 (85)	10.7 (86)	2 (50)	4.8 (9)	1 (33)	0.1 (2)	7 (100)	28.7 (18)
Misc. items[d]	4 (22)	24.9 (3)	1 (25)	1.1 (2)	1 (25)	3.8 (4)	4 (57)	11.8 (7)

[a] Percent of samples. Note that frequencies of insect groups are relative to total insect sample.
[b] Percent of combined volumes. Volume percentages of insect groups are relative to total insect volume.
[c] Includes Coleoptera, Homoptera, Odonata, Ephemeroptera, Diptera, and unidentified insect parts.
[d] Includes 3 frogs (*Rana pipiens*), 4 samples of grain, and miscellaneous debris (soil particles, gravel).

obervations of feeding in dumps by a variety of species (Sibly and McCleery 1983a, see Burger and Gochfeld 1983 for other references) few studies have examined the use of dumps during the breeding season versus alternate sources of food (Southern et al. 1976, Sibly and McCleery 1983b). Use of dumps was constant, but minimal in my study area (Table 1), with daily maxima at all major sites totalling less than 5% of the estimated breeding population for any given month. Weseloh et al. (1983) recorded no use of dumps by Ring-billed Gulls from mid-April to mid-July in the Lower Great Lakes, with an increase in dump use in July and August. Blokpoel and Tessier (1986) reviewed five other studies of Ring-billed Gull diets in the Great Lakes and St. Lawrence region during the breeding season, and in only one of seven locations was garbage cited as one of the main dietary constituents. In an Alberta population, Vermeer (1970) recorded a low incidence of refuse in May and June diets and a predominance in July. I did not determine whether a small number of gulls on my study area were specializing on refuse feeding (Hunt 1972).

During periods of rainfall when cultivated fields were too wet for tillage, earthworms became available on pastures throughout the day and were fed upon by gulls (cf. Andersson 1970, Sibly and McCleery 1983b).

Late June represented a transitional period in available foraging habitat. By this time most tilling activities were finished, and farmers began to cut the first crop of hay. Gulls followed the haying implements that flushed and injured small birds, rodents, and insects. Large aquatic insect hatches provided an additional food source along lake shores at this time.

Diet.—The wide variety of food items in gull stomachs in this study confirms what has been found in other populations of Ring-billed Gulls (Vermeer 1970, Baird 1976, Jarvis and Southern 1976, Southern et al. 1976). The population at Dog Lake appears to differ from several others studied to date in that few fish were taken (cf. Jarvis and Southern 1976, Southern et al. 1976, Haymes and Blokpoel 1978). Only traces of fish were found in stomach contents, even though Dog Lake and particularly Lake Manitoba support sizeable populations of fish-eating Common Terns (*Sterna hirundo*), American White Pelicans (*Pelecanus erythrorhynchos*), and Double-crested Cormorants (*Phalacrocorax auritius*) (Koonz and Rakowski 1985).

Similarly, chick regurgitations in this study varied considerably from those reported in the Great Lakes regions where fish are the principal food source (Haymes and Blokpoel 1978, Kirkham and Morris 1979). In Alberta, on the other hand, arthropods were the dominant food type in June, and refuse the chief food in July both for adults and chicks (Vermeer 1970). The Dog Lake Ring-billed Gulls may have become "local specialists" (Fox and Morrow 1981) that forage mainly in agricultural areas.

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SHORT COMMUNICATIONS

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Brood division and postnesting behavior of Flammulated Owls.—The Flammulated Owl (*Otus flammeolus*) is widely distributed in the montane forests of western North America (Bent 1938). The owl is insectivorous (Ross 1969) and is presumed to be migratory in the northern part of its range (Balda et al. 1975). Little is known of the nesting behavior of this species, especially during the postfledging period. Here, we present the postfledging behavior of adults and young and describe the occurrence of brood division in Flammulated Owls.

Study area.—The study was conducted on a 452-ha area of the Manitou Experimental Forest, Teller County, in central Colorado. Elevation of the study tract was 2700 m. Forests consisted of old-growth stands (>200 years) of ponderosa pine (*Pinus ponderosa*) mixed with Douglas-fir (*Pseudotsuga menziesii*) (58% coverage of the total area), young (<100 years) stands of Douglas-fir mixed with blue spruce (*Picea pungens*) (27% of the area), mature (100–200 years) stands of quaking aspen (*Populus tremuloides*) mixed with blue spruce (11%), mature aspen stands (>75 years) (3%), and meadow (1%). The understory vegetation and topography of the study tract were described by Reynolds et al. (1985). Also included are observations of a single pair of Flammulated Owls (MN1-83) that nested in similar habitat 52 km north of the study tract.

Methods.—Five families of owls (2 in 1982; 3 in 1983) were studied from the time the young left the nest in late July until we lost contact with the owls or until they left the area in October. Four adult males were equipped with backpack or tail-mounted transmitters, and 2 adult females and 6 of 14 young were equipped with backpack transmitters within one day of fledging (Reynolds and Linkhart 1984). Although all members of brood subgroups (see below) were not radio-tagged, 7 of 10 subgroups had at least 1 member (adult or fledgling) with a transmitter. Although the effects of transmitters on adults and young were unknown, affixing transmitters did not lower the annual return rate of adult males to the study tract, or the nesting success of radio-tagged pairs (Linkhart et al., in review). The movements and behavior of three families were monitored until the young were lost or killed by predators (1–12 nights after fledging). Two families were monitored until the owls left the study tract in the late summer and fall. Of the four other families that were studied, three were lost immediately after fledging (radio failure), and all of the fledglings of one pair were lost to a Sharp-shinned Hawk (*Accipiter striatus*) before we began postfledging monitoring. The nightly postfledging behavior of families was observed for a total of 24 h in 1982 (35% between 20:00–22:00 h MST; 35% between 22:00–24:00 h; 17% between 24:00–02:00 h; 13% between 04:00–06:00 h), and a total of 42 h in 1983 (27% between 20:00–22:00 h; 49% between 22:00–24:00 h; 7% between 24:00–02:00 h; 17% between 04:00–06:00 h). Movements and day roosts were determined by locating radio-tagged owls with a portable radio receiver and hand-held yagi antenna. Families of owls were observed continuously for 1–3 h at a time.

Results.—Mean brood size of the 5 families was 2.8 young (1 of 2 young, 4 of 3 young). Fledging of all young occurred within 1 h after sunset, and all broods fledged over 2 nights. Each of the 5 broods had divided into 2 subgroups by the third night after the first young fledged; 1 subgroup being tended only by the male and the other only by the female. However, because 2 adult females could not be captured, we were unable to continue monitoring their subgroups. In both of these situations, the broods involved had undergone the initial stages of brood separation—brood subgroups were separated by a minimum of 80 m, and the adults of both were strongly, if not completely, associated with their respective subgroups. Brood subgroups consisted of single owlets or siblings that left the nest the same night. There

was no pattern in which a parent associated with a specific subgroup; in 3 broods, the first bird to fledge was tended by the female, and in the other two, the first to fledge was tended by the male. The sex of fledglings was not determined.

Subgroups dispersed from their nests in different directions, and subsequent contact between them was not observed during the remainder of the fledgling dependency period. A typical example of the process of division was as follows: The 1 young of A10-82 brood (3 young) that fledged on 23 July formed 1 subgroup, and the remaining 2 young, which fledged on the following evening, formed the second subgroup. We observed this family for 2 h beginning at sunset (20:18 h) on 23 July. The female tended the first fledgling immediately after it left the nest (21:05 h). She continued, however, to assist the male in feeding the two young that remained in the nest. During the 2 h period, the male delivered (21:45 h) only one prey item to the single fledged young, considerably less than a nightly mean of 9.9 deliveries/h males at this and 12 other nests made during the nestling period (Reynolds and Linkhart, in press). Three nights later, the male was feeding only the 2 young that fledged on 24 July and was not assisted by the female. These 2 subgroups remained within 50 m of each other for six nights after fledging, at which time the female and her subgroup disappeared.

During the first 2 weeks after fledging, the day-roost trees of brood subgroups and tending adults were close together, and during the first week after fledging, these roosts were within 100 m of their nests. To demonstrate this general pattern, we present the distances between the day roosts of A4-83 male and his single fledgling. During the first 13 days after fledging, the distance between their day roosts was less than 35 m ($\bar{x}$ = 18 ± 14 m [SD], range = 0–32, N = 9), after which the distance began to increase daily. During the next 20 days, the mean distance between day roosts was 227 ± 146 m (range = 0–585, N = 18). The mean distance to the nest from the roosts of the male during the first seven days (23–29 July) was 47 ± 27 m (range = 14–74, N = 5). After the first week and through the remainder of the postfledging period, subgroups moved to 250–800 m from the nest. During this period, the fledglings and the adult of 1 subgroup wandered through the home ranges of several adjacent pairs. Throughout the postfledging period, the distance between day roosts of members of a subgroup was small, and they often roosted in the same tree (see below).

During the first 5 nights after fledging, adults foraged in the vicinity of the fledglings and delivered food to them every 1–5 min during the first hour after sunset and more sporadically later in the night. By 7–10 nights after leaving the nest, fledglings made attempts to glean insects from the ground. During this latter period, fledglings followed adults during foraging trips, which gradually increased in distance and duration as the flight capabilities of fledglings improved. Fledglings ceased moving by about 22:00 h, but the adults continued to feed them. Just before dawn, additional, although less extensive foraging movements involving the fledglings took place. These culminated with owls going to roost approximately one-half hour before sunrise. Fledglings begged for food 5–15 times/min during early evening and morning foraging periods, but vocalized less frequently during the middle of the night. Food-begging ceased altogether when owls went to roost.

By 20–25 nights after fledging, adults spent little time in the vicinity of fledglings during the night and only occasionally provisioned them with food. By 25–32 nights after fledging, the young were no longer provisioned with food and only occasionally gave food-begging vocalizations while foraging. After independence, fledglings continued to forage most intensively in the early evening (between 20:30–22:00 h). Subgroup members foraged within 50 m of each other and gleaned insects from the crowns and trunks of live trees, from snags, and from the ground. By the middle of the night, foraging occurred at irregular intervals. A second intensive foraging bout occurred in the last 2 h before dawn.

We monitored 2 brood subgroups (separate families) until the young dispersed from the

study tract. Two fledglings of A15-82 were last observed on 28 August, 35 nights after fledging. Both transmitters may have failed on this night, but the foraging and flight capabilities of the fledglings and subsequent wide searches for the owlets suggested that they dispersed from the study tract. Moreover, mean distance between the day-roost trees of these 2 fledglings for 3 days prior to 28 August ($\bar{x}$ = 98 ± 46 m, range = 61–150, N = 3) was considerably more than the distance between their day roosts prior to 25 August ($\bar{x}$ = 5 ± 6 m, range = 0–14, N = 13). Radio contact with a second subgroup (single fledgling of A4-83) was lost 33 nights after fledging (25 August). This owlet flew well and was foraging successfully.

One adult male (A4-83) was monitored into the fall. This male was last observed on 12 October and had increased in body weight by 20% during the 23 days from 13 September (56.5 g) to 6 October (67.5 g). Also, during the last 5 days of his residence, the male changed his day-roosting behavior by abandoning his favored roosts during the previous month (all within his nesting home range) for roosts that were increasingly farther from his home range and toward the southwest.

Discussion.—Brood division, in which part of the brood is tended by the male and part by the female, is best known in precocial birds (e.g., Tuck 1972, Simmons 1974, Horsfall 1984). Recent studies of altricial birds (e.g., Smith and Merkt 1980, Moreno 1984, McLaughlin and Montgomerie 1985) indicate that brood division may be common in birds with biparental care. Our results are the first to demonstrate brood division in strigiforms.

Within altricial species where brood division occurs, its establishment appears to require varying amounts of time after fledging. Flammulated Owl fledglings passed through what we term a "brood separation phase," in which the fledglings gradually separated but continued to be tended by both adults. What has been variously termed as stable brood division (McLaughlin and Montgomerie 1985), complete division of labor (Smith 1978), or simply brood division (Edwards 1985) occurred when, perhaps due to the increasing distance between brood subgroups, each adult becomes conditioned to associate with a single subgroup (see Smith 1978). Published accounts indicate that for Song Sparrows (*Melospiza melodia*), the "brood separation phase" lasts 5 days (Smith and Merkt 1980), for Northern Wheaters (*Oenanthe oenanthe*) 3–8 days (Moreno 1984), for Eurasian Blackbirds (*Turdus merula*) 0–10 days (Edwards 1985), and for Prairie Warblers (*Dendroica discolor*) (Nolan 1978) and Lapland Longspurs (*Calcarius lapponieus*) less than 1 day (McLaughlin and Montgomerie 1985). In Flammulated Owls, brood separation began with the fledging of the first young in a brood, and brood division had occurred by two nights after the fledging of the last young.

McLaughlin and Montgomerie (1985) reviewed five possible benefits of dividing broods: (1) minimizing losses to predators, (2) increasing foraging efficiency, (3) helping young learn to forage, (4) facilitating differential dispersal of the sexes, and (5) promoting sexual imprinting and mate choice. In Flammulated Owls, we suspect that brood division might reduce predation on the young. First, food begging of the fledglings was frequent, and more pronounced (facilitated) when fledglings were in the same area. Dividing broods into small segments might reduce vocalizations and possibly losses to nocturnal predators. Second, because owlets in subgroups day-roosted close to one another (making them more obvious), and all known cases of predation on owlets occurred during the day, losses of whole broods could be reduced by dividing and separating broods. Alternatively, brood division may simply be the result of the timing of fledging. Because the broods we studied fledged over two nights, the limited mobility of the owlets during the evening of fledging may have forced them to associate with siblings that left the nest the same night (see also Smith and Merkt 1980). Whether brood division occurs in broods all of whose members fledge in the same night is unknown.

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Species-area relationships of winter residents in isolated woodlots.—The number of bird species breeding within woodlots or using woodlots temporarily during migration is strongly correlated with woodlot area (e.g., Martin 1980, Ambuel and Temple 1983, Blake 1986).

Species-area relationships of winter bird communities, however, have received little attention (Haila 1981), despite potentially strong effects of forest area on both weather severity and food availability (Forman and Godron 1981).

Woodlots in east-central Illinois are isolated from each other by cropland, and the transition from bare ground to woodlot vegetation is generally sharp, thus forming distinct patches of habitat. Here I examine relationships between area of isolated woodlots in east-central Illinois and number of species of birds found in these woodlots during winter. Species-area relationships are compared among trophic groups to examine potential effects of variation in availability of food resources among communities.

Methods.—I censused 5 woodlots during the winter of 1979–80 to gain a preliminary assessment of the species-area effect. Eleven woodlots, ranging in size from 1.8 to 600 ha, were censused during the winter of 1980–81 to include a greater variety of sizes. Number and choice of woodlots were dictated by the landscape of east-central Illinois. Only woodlots that possessed a relatively mature canopy and well-developed understory, showed no evidence of recent, heavy disturbance, and were surrounded by nonforest habitat were included.

I surveyed birds using the point-count technique (Ferry and Frochot 1970). I visited each observation point for 10 min during a census and recorded all birds seen or heard within or below the canopy. Survey points were at least 150 m apart. Each woodlot was censused 3 or 4 times during December–February of each year.

Number of observation points increased with area in order to obtain a reasonably complete count of species present in larger woodlots. Total number of species recorded generally increases with sample effort, but at some point additional observations do not increase the species total. Species accumulation curves (cumulative number of species plotted against number of observation points) reached or approached an asymptote for all woodlots, indicating that species richness of woodlots was determined adequately (Blake and Karr 1982).

I conducted censuses from sunrise until 2.5 h after sunrise on days with little or no wind and no precipitation in order to minimize potential confounding effects of weather. In addition, I censused woodlots in an order unrelated to woodlot area, thereby reducing potential effects of weather on the species-area relationship.

I analyzed species composition on the basis of both migratory status and primary foraging habit. I used Kendeigh (1982) as the primary guide for assigning species to categories (permanent residents, winter residents, transients) based on their status in east-central Illinois. Some species fell into two categories. For example, low permanent resident populations of some species (e.g., Brown Creeper [*Certhia americana*]) are augmented during winter by individuals that breed farther north. Transients overlap temporally with permanent and winter residents but do not normally remain in east-central Illinois throughout winter.

I divided species according to primary food type and foraging location (Martin et al. 1951, Williams and Batzli 1979). Species that used two types of food or locations in approximately equal proportions were assigned ½ to each group. Categories included granivores, insectivores that obtain insects from the bark of trunks and large limbs (by drilling or gleaning), insectivores that glean insects from small twigs and brush piles, frugivores, and sapsuckers.

I evaluated species-area relationships according to the exponential function rather than the power function, because the former model accounted for a greater amount of variation in species number (Blake and Karr 1982) and because the exponential function resulted in a better fit. No data set departed from normality.

Summary data on temperature and snowfall for the winters of 1979–80 and 1980–81 were obtained from the State Water Survey Division, Illinois Department of Energy and Natural Resources (Table 1).

Bird community composition.—Thirty-one species of birds were recorded during winter in one or more of the 11 woodlots in east-central Illinois, 19 in 1979, and 30 in 1980 (Appendix 1). Species present on small islands were, in almost all cases, also present on

TABLE 1

MONTHLY TEMPERATURE AND PRECIPITATION DATA FOR THE MONTHS OF NOVEMBER–FEBRUARY 1979–80 AND 1980–81 IN EAST-CENTRAL ILLINOIS

	1979–80				1980–81			
	Nov.	Dec.	Jan.	Feb.	Nov.	Dec.	Jan.	Feb.
Mean maximum temperature (°C)	9.1	7.1	0.7	−1.1	10.1	5.9	−0.1	4.3
Mean minimum temperature (°C)	0.5	−2.9	−6.8	−8.4	0.5	−4.2	−8.4	−5.8
Precipitation (mm)	68.8	29.0	19.6	43.2	41.4	34.8	16.3	56.1

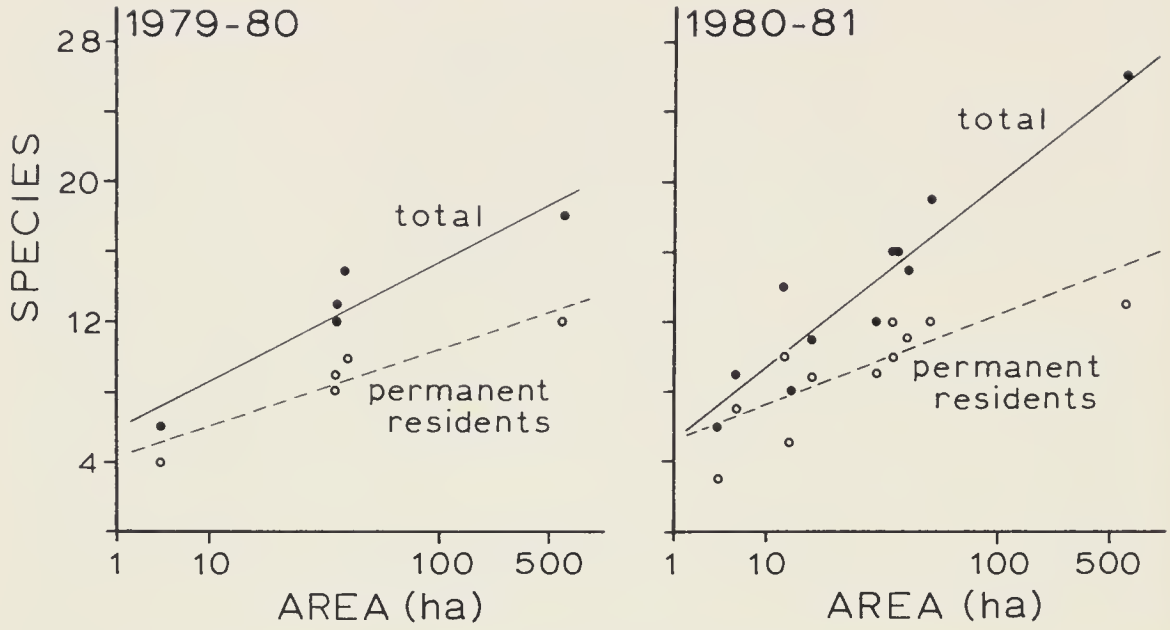

FIG. 1. Total number of species and number of permanent resident species recorded during winters of 1979–80 and 1980–81 plotted against area (log scale) of woodlots. Solid circles and lines refer to total species number, and open circles and dashed lines refer to permanent residents. Lines were fitted by linear regression (exponential model) (see Table 3).

larger islands. Greater species numbers in 1980 were partially due to the larger number of woodlots surveyed, and, apparently, also to a higher number of transients in 1980; numbers of resident species were more similar between years (Appendix 1) (Fig. 1).

Granivores feeding on small seeds were the dominant trophic group, in terms of number of species, in all woodlots (Table 2). Seed eaters showed the greatest change between years, both at individual woodlots and overall, but, in general, more species were present in larger woodlots. Three species relying on acorns as a primary food were uncommon or absent in the smallest woodlots, but all were present in all woodlots greater than 5 ha. Number of species taking insects from bark, either by drilling into or gleaning from the surface, also was greater in larger woodlots (Table 2). This was particularly true for species gleaning insects from trunks and those gleaning insects from small twigs.

Species-area relationships.—Total number of species correlated strongly with area in both winters (Fig. 1) (Table 3). The rate of increase (slope) in species number with area was higher in 1980, but not significantly so (t-test, $P > 0.05$). The higher slope in 1980 was a result of greater species totals in larger rather than small woodlots, and intercepts did not differ ($P > 0.05$) between years. Results did not differ between years when I recalculated the species-area relationship for 1980 using only those woodlots censused in both 1980 and 1979. Number of permanent residents correlated significantly with area in both years (Fig. 1) (Table 3), and the results did not differ significantly between years.

I combined all granivores and all bark insectivores into two groups to examine correlations with area. Bark insectivores correlated significantly with area in 1979 and 1980, but granivores showed a significant correlation only in 1980 (Table 3). The species-area intercept was higher for granivores than for bark insectivores in both years (1979: $t = 2.13$, df = 8, $0.10 > P > 0.05$; 1980: $t = 2.83$, df = 20, $P < 0.02$), reflecting the greater number of granivore species in all woodlots.

Discussion.—Woodlots in east-central Illinois provide valuable habitat for birds during

TABLE 2
SPECIES NUMBERS IN DIFFERENT TROPHIC GROUPS

Trophic group	Woodlot size (ha)										
	1.8	2.3	4.7	5.1	6.5	16.2	24	24	28	40	600
1979											
Granivores											
Small seeds	3						3.5	5	4		5
Acorns	1						3	3	3		3
Insectivores											
Bark drill	1						2.5	2.5	2.5		2.5
Trunk glean	1						1.5	1	2.5		3
Twig glean									1.5		2.5
Frugivores							1.5	1.5	1.5		1.5
Sapsucker											0.5
1980											
Granivores											
Small seeds	4	4	5	3	4	4	6.5	6.5	6	6	10
Acorns		2	3	2	3	3	3	3	3	3	3
Insectivores											
Bark drill	1	1	1.5	1.5	1	1.5	2.5	2	1.5	2.5	2.5
Trunk glean	1	1	1.5	1	1	1	1.5	1.5	1.5	2.5	2
Twig glean		1	1.5	0.5	2	1.5	1.5	1	1.5	1.5	3
Frugivores			1.5	0.5	2	1.5	1.5	1	1.5	1.5	3.0
Sapsucker											0.5

breeding and migration seasons, and area of the woodlots influences the number of species that use them at these times (Blake and Karr 1984, Blake 1986). Woodlot size also influences winter bird populations. Permanent residents varied with area in the same way between seasons; no difference in the species-area relationship was apparent beween summer and winter for this group (Blake 1983 for summer data).

Although habitat structure influences composition of many bird communities (Cody 1985), differences in habitat among forest patches appear to exert little influence on bird species richness of woodlots—relative to the influence of area—at least in cases where habitat heterogeneity does not increase markedly with area (Blake and Karr 1982, Ambuel and Temple 1983, Blake 1983). Woodlots censused during this study were selected initially partially on the basis of general similarity in vegetation. Differences in habitat occurred among woodlots, but such differences were not correlated with area of woodlots (Blake and Karr 1982). Also, various aspects of habitat structure did account for some additional variation in number of bird species during the winter of 1980–81 (Blake and Karr 1982) but much less than that accounted for by area.

A lack of correlation between species numbers and habitat variables does not necessarily indicate that habitat structure does not influence bird communities of isolated woodlots. Environmental variation certainly is expected to increase as area increases and may account for much of the species-area effect (Williamson 1981). However, such variation may be apparent on a different scale or may involve factors (e.g., soil types) that typically are not

TABLE 3

RESULTS OF SPECIES-AREA REGRESSIONS (SEMI-LOG)

Species group	1979–80				1980–81			
	Intercept	Slope	r^2	P	Intercept	Slope	r^2	P
Total species	6.0	2.04	0.900	<0.012	5.2	3.18	0.902	<0.0001
Permanent residents	4.1	1.36	0.891	<0.014	5.2	1.53	0.648	<0.001
Granivores	4.5	0.66	0.687	<0.08	4.2	1.42	0.853	<0.0001
Bark insectivores	1.3	1.05	0.803	<0.037	2.1	0.89	0.829	<0.0001

measured. An increase in environmental heterogeneity may, by providing a greater variety of resources, allow a greater number of species to coexist. Similarly, differences in area among woodlots may influence the amount of some critical habitat present, resulting in stochastic loss of some species from smaller woodlots (Williamson 1981). Loss of critical microhabitats or refugia, required during periods of stress, is a probable cause of species loss from some islands (Karr 1982).

Habitat structure may influence species distribution patterns during winter through effects on weather and food resources. Unusually severe weather may cause major reductions in winter bird populations, as occurred during the winter of 1976–77 in southern Illinois (Graber and Graber 1979). Vegetation moderates the influence of weather, particularly wind, and the microenvironment within the center of a large forest is less severe and less variable than at the center of a small woodlot (Forman and Godron 1981). In a large forest, birds may concentrate their activities in areas that provide protection from weather (Carpenter 1935), an option that is not as readily available in small woodlots. Low temperatures and high winds cause some species to shift foraging locations from exposed to more protected sites as weather becomes more severe (Grubb 1975). Small forests may not provide sufficient cover to allow such behavioral flexibility.

The greater number of species in larger forests also occurs because large forests may support bird species that are dependent on spatially variable food supplies (e.g., Red-headed Woodpecker [Graber et al. 1977]). The irregular occurrence of frugivores (e.g., Cedar Waxwing) in large woodlots and their absence from small woodlots probably reflects this effect.

Haila (1981) reported berry and seed eaters on very small islands during winter; such species were considered habitat generalists, moving among islands and habitats in search of available and patchily distributed food resources. In the present study, however, woodlots generally were well-separated, and species richness was not correlated with measures of forest isolation (Blake and Karr 1982). Insectivorous birds, which are more dependent on specific habitat requirements and predictable food supplies (Haila 1981), are more dependent on large woodlots, which provide greater availability of these foods. Few insectivores occurred in small woodlots during winter in east-central Illinois, but numbers increased strongly with woodlot area. Higher species totals for granivores, as compared to bark insectivores, in small woodlots probably reflects the fact that granivores may forage in nonwooded habitat near woodlot borders, if such habitat exists. At the same time, the correlation between granivores and area reflects the greater foraging area and the better microenvironmental conditions for granivores both around and within large woodlots.

For species that winter in Illinois and other heavily disturbed regions, habitat that provides sufficient shelter and food may be in short supply, and isolated woodlots may be an important refuge during winter. The importance of habitat islands to bird populations extends beyond the breeding season, and additional, more detailed studies during nonbreeding seasons are needed.

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Appendix 1

Species Recorded (+) in Woodlots in East-central Illinois during Winters of 1979–80 and 1980–81

Species	Trophic group[a]	Migratory status[b]	1979	1980	Smallest woodlot (ha)
Mourning Dove (*Zenaida macroura*)	GS	WR-T		+	1.8
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	GA	PR	+	+	2.3
Red-bellied Woodpecker (*M. carolinus*)	GA	PR	+	+	4.7
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	S-BGT	T-WR	+	+	600
Downy Woodpecker (*Picoides pubescens*)	BD	PR	+	+	1.8
Hairy Woodpecker (*P. villosus*)	BD	PR	+	+	24
Northern Flicker (*Colaptes auratus*)	F-BD	PR-T	+	+	4.7
Blue Jay (*Cyanocitta cristata*)	GA	PR	+	+	1.8
Black-capped Chickadee (*Parus atricapillus*)	BGB	PR	+	+	2.3
Tufted Titmouse (*P. bicolor*)	BGB-GS	PR	+	+	4.7
Red-breasted Nuthatch (*Sitta canadensis*)	BGT	T-WR	+	+	28
White-breasted Nuthatch (*S. carolinensis*)	BGT-GS	PR	+	+	4.7
Brown Creeper (*Certhia americana*)	BGT	PR-WR	+	+	1.8
Carolina Wren (*Thryothorus ludovicianus*)	BGB	PR	+		600
Winter Wren (*Troglodytes troglodytes*)	BGB	T-WR		+	600
Golden-crowned Kinglet (*Regulus satrapa*)	BGB	T-WR		+	24
Ruby-crowned Kinglet (*R. calendula*)	BGB	T-WR		+	600
American Robin (*Turdus migratorius*)	F	T-PR	+	+	4.7
Cedar Waxwing (*Bombycilla cedrorum*)	F	PR		+	6.5
European Starling (*Sturnus vulgaris*)	GS	PR	+	+	1.8
Yellow-rumped Warbler (*Dendroica coronata*)	F-BGB	T-WR		+	600
Northern Cardinal (*Cardinalis cardinalis*)	GS	PR	+	+	1.8
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	GS	PR-T		+	600
American Tree Sparrow (*Spizella arborea*)	GS	WR-T		+	2.3
Song Sparrow (*Melospiza melodia*)	GS	PR-T		+	600

Appendix 1
Continued

Species	Trophic group[a]	Migratory status[b]	1979	1980	Smallest woodlot (ha)
White-throated Sparrow (*Zonotrichia albicollis*)	GS	T-WR		+	600
Dark-eyed Junco (*Junco hyemalis*)	GS	WR	+	+	1.8
Red-winged Blackbird (*Agelaius phoeniceus*)	GS	T-WR		+	1.8
Purple Finch (*Carpodacus purpureus*)	GS	T-WR	+	+	24
American Goldfinch (*Carduelis tristis*)	GS	PR	+	+	2.3
House Sparrow (*Passer domesticus*)	GS	PR		+	1.8

[a] Trophic groups include granivores that eat small seeds (GS) or acorns (GA); insectivores that drill in bark (BD), that glean trunks and large branches (BGT), or that glean small twigs and brush piles (BGB); frugivores (F); and sapsuckers (S).
[b] Migratory status includes permanent residents (PR), winter residents (WR), and transients (T). Some species fit into more than one category.

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Bark-foraging bird abundance unaffected by increased snag availability in a mixed mesophytic forest.—Snags are an important habitat component for many bird species, and low snag availability may adversely affect populations of birds that nest in or forage on snags (Balda 1975, Thomas et al. 1979). Silvicultural practices such as even-aged management, short stand rotation, and removal of cull trees reduce natural snag densities.

Snags can be provided for birds by managing old-growth forest or by leaving snags during timber harvest. Snags also can be created using herbicides, topping, and girdling to increase snag availability in managed stands (Bull and Partridge 1986). Studies of how bird density responds to snag availability mainly have been correlative and not experimental. Dickson et al. (1983) demonstrated experimentally that snag density in clearcuts influenced the abundance of some cavity-nesting and bark-foraging birds. Carey (1983) and Sedgwick and Knopf (1986) suggested that snags are not as important as dead and dying portions of live trees for cavity-nesting and bark-foraging birds in some unmanaged hardwood stands.

We examined the response of bark-foraging birds to increased snag availability created by herbicide injection and topping. Our null hypothesis was that bark-foraging bird abundance during the winter and breeding seasons would not be affected by doubling snag density in a hardwood forest.

Study area and methods.—The study was conducted in 2 watersheds in Robinson Forest, Breathitt County, Kentucky. Robinson Forest was heavily cut until 1920, and the vegetation is a second-growth mixed mesophytic forest. Pitch pine (*Pinus rigida*), chestnut oak (*Quercus prinus*), and scarlet oak (*Q. coccinea*) dominate the ridge tops. South-facing slopes are dominated by hickory (*Carya* spp.), white oak (*Q. alba*), black oak (*Q. velutina*), and sourwood (*Oxydendrum arboreum*); and north-facing slopes are dominated by northern red oak (*Q. rubra*), yellow-poplar (*Liriodendron tulipifera*), basswood (*Tilia* spp.), and cucumbertree (*Magnolia acuminata*). American beech (*Fagus grandifolia*) and eastern hemlock (*Tsuga canadensis*) are common along drainages.

A 20-ha study area was established in each of 2 watersheds in 1980. Both watersheds are similar in size and exposure, and have similar vegetative and faunal communities (Moriarty 1982).

In July 1982, 360 trees were selected for herbicide treatment in one watershed (TSI) in an attempt to at least double snag density based on Moriarty's (1982) pretreatment estimates. Trees suitable for injection were ≥ 10 cm dbh (diameter at breast height) and >5 m tall, thus meeting minimum snag requirements for most cavity-nesting birds (Conner 1978, Evans and Conner 1979). Six tree taxa were chosen for herbicide injection: American beech, eastern hemlock, yellow-poplar, chestnut oak, scarlet oak, and yellow pines (*Pinus* spp.). The selection of 3 mesic-site and 3 dry-site tree taxa resulted in a fairly uniform distribution of herbicide-created snags over the 20-ha area.

Sixty trees of each taxon were injected with TORDON 101R (mention of trade names does not imply endorsement by the Kentucky Agricultural Experiment Station), a picloram herbicide (4-amino-3,5,6-trichloropicoline acid). TORDON was selected based on its low toxicity to avian and mammalian species (Hudson et al. 1984), and its common use in silvicultural practices (U.S. Forest Service 1984). One-half of the injected trees, 30 of each taxon, were randomly selected and topped using chain saws and bow saws. Topping was used in combination with herbicide injections to simulate broken tops which may be important avenues of heart-rotting fungi (McClelland and Frissell 1975). Trees were topped at 8.8 m (30 ft) to satisfy the average snag height requirements for most cavity-nesting birds (Conner 1978). Herbicide injection and topping were completed in August 1982.

Winter and breeding birds on the TSI and control areas were counted using a line transect

method (Conner and Dickson 1980). Birds were counted along 5 equidistant, parallel, 360-m transects in each watershed, consistent with 1981 pretreatment sampling (Moriarty 1982). Bird species and number of individuals (detected by sight or sound) were recorded up to 50 m from each transect and allowed sampling without overlap. The 50-m boundaries of each transect were marked to reduce the risk of counting the same birds on adjacent transects. Birds were counted 8 times during winter (January–March) and 6 times during breeding seasons (May–June) of 1981, 1983, 1984, and 1985. In 1981, winter birds were counted within 3 h of sunrise (4 times) and 3 h of sunset (4 times) on each watershed by one observer. From 1983 to 1985 winter birds were counted within 3 h of sunrise (8 times) by a different observer. Breeding birds were counted within 3 h of sunrise (3 times) and 3 h of sunset (3 times) all 4 years. No counts were conducted during adverse weather conditions such as heavy rain or snow, high winds, or fog.

Only bark-foraging bird species with a detection frequency ≥20% and an average density of ≥0.1/10 ha were included in this analysis. Mean numbers of each bird species were averaged for each transect and compared between watersheds (df = 1) and among years (df = 3). Treatments were not replicated; transects represent 5 independent samples per area. A split-plot analysis was used to detect trends in abundance of winter and breeding bark-foraging bird species and on abundance of total bark-foragers of all species with time as the split plot variable. The General Linear Models procedure in the Statistical Analysis System was used to test (1) the pretreatment minus average posttreatment by watershed interaction, (2) the first year posttreatment minus subsequent average posttreatment by watershed interaction, and (3) the second year posttreatment minus third year posttreatment by watershed interaction (SAS Institute 1982). Significant ($P < 0.05$) opposing trends were necessary to detect effects of the treatment on bird abundance. Duncan's Multiple Range (DMR) tests were also used to detect differences in bird abundance between watersheds within years.

Snag abundance.—Snag density increased on the TSI area from 14.8 snags/ha in 1981 (Moriarty 1982) to 32.8 snags/ha in 1983. Snag density on the control area averaged 18.0 snags/ha (Moriarty 1982). Prior to TSI, snag densities in both watersheds were low compared with similar forests in the eastern United States (Carey 1983, McComb and Muller 1983).

Bird abundance.—Average abundance of winter bark-foraging birds did not increase significantly following treatment on the experimental area relative to the control area ($P > 0.05$). Average abundance of winter bark-foraging birds on the TSI area was 4.4/10 ha in 1983 and 3.9/10 ha in 1984, while average abundance on the control area was 3.0 and 2.8 bark foragers/10 ha in 1983 and 1984, respectively (DMR, $P < 0.05$) (Table 1). Bark-foraging bird abundance did not differ (DMR, $P > 0.05$) between watersheds during 1985. Although average bark-forager abundance was statistically higher on the TSI area for the first 2 years posttreatment, this relationship was not consistent over species within the guild and as such is of questionable biological significance (Mannan et al. 1984). Proportional changes from pretreatment conditions were similar between the treated and control watersheds. Division of posttreatment values by pretreatment values for winter bark-foragers results in 2.2, 2.0, and 1.6 more birds each year posttreatment on the TSI area; corresponding values for the control area were 2.3, 2.1 and 2.6. High posttreatment density estimates relative to the pretreatment estimates is likely a function of the sampling technique; pretreatment winter counts were conducted in the morning and evening while posttreatment counts were conducted exclusively in the morning. Relative abundance of bark-foragers in the breeding season was not significantly different between the TSI and control area ($P > 0.05$), or among years (Table 1). There were no significant treatment effects ($P > 0.05$) on any winter or breeding bird species presented in Table 1.

Although no significant increase in bark-forager abundance was observed, evidence of

TABLE 1

AVERAGE ABUNDANCE OF BARK-FORAGING BIRDS PER 10 HECTARES ON THE EXPERIMENTAL AND CONTROL WATERSHEDS, BREATHITT COUNTY, KENTUCKY (N = 5 TRANSECTS/WATERSHED/YEAR)

Species	Experimental watershed				Control watershed			
	1981[a]	1983	1984	1985	1981[a]	1983	1984	1985
Winter species								
Pileated Woodpecker (*Dryocopus pileatus*)	0.7 (0.2)[b]	0.4 (0.2)	0.6 (0.2)	0.4 (0.3)	0.6 (0.2)	0.5 (0.2)	0.4 (0.1)	0.6 (0.2)
Hairy Woodpecker (*Picoides villosus*)	0.9 (0.2)	1.9 (0.6)	1.5 (0.3)	1.2 (0.3)	0.4 (0.3)	1.4 (0.2)	1.1 (0.1)	1.5 (0.3)
Downy Woodpecker (*P. pubescens*)	0	0.5 (0.3)	0.5 (0.2)	0.1 (0.1)	0	0.2 (0.1)	0.5 (0.2)	0.4 (0.2)
Red-bellied Woodpecker (*Melanerpes carolinus*)	0	0.2 (0.1)	0.1 (0.1)	0.1 (0.1)	0	0.3 (0.2)	0.1 (0.1)	0.1 (0.1)
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	0	0.1 (0.1)	0.3 (0.2)	0	0	0	0.2 (0.1)	0.1 (0.1)
White-breasted Nuthatch (*Sitta carolinensis*)	0.3 (0.1)	1.3 (0.4)	0.9 (0.4)	1.2 (0.6)	0	0.6 (0.1)	0.5 (0.4)	0.9 (0.4)
Brown Creeper (*Certhia americana*)	0.1 (0.1)	0	0	0.1 (0.1)	0.3 (0.2)	0	0	0
Winter total	2.0	4.4	3.9	3.1	1.3	3.0	2.8	3.6
Breeding species								
Pileated Woodpecker	1.0 (0.4)	0.9 (0.5)	0.6 (0.3)	0.2 (0.1)	0.8 (0.2)	0.6 (0.2)	0.5 (0.2)	0.8 (0.2)
Hairy Woodpecker	0.9 (0.3)	0.8 (0.3)	0.7 (0.4)	0.2 (0.1)	0.4 (0.2)	0.3 (0.2)	0.4 (0.2)	0.3 (0.1)
Downy Woodpecker	0	0.1 (0.1)	0.4 (0.2)	0.2 (0.2)	0	0	0.3 (0.2)	0.4 (0.3)
Red-bellied Woodpecker	0.3 (0.2)	0.3 (0.2)	0.5 (0.2)	0	0.1 (0.1)	0.2 (0.1)	0	0
White-breasted Nuthatch	0.5 (0.2)	0.6 (0.1)	0.2 (0.2)	0.3 (0.1)	0.3 (0.2)	0.5 (0.2)	0.3 (0.2)	0.6 (0.3)
Black-and-white Warbler (*Mniotilta varia*)	2.1 (0.6)	1.5 (0.6)	2.2 (0.8)	1.5 (0.4)	1.5 (0.2)	1.4 (0.3)	1.8 (0.6)	1.3 (0.4)
Breeding season total	4.8	4.2	4.6	2.4	3.1	3.0	3.3	3.4

[a] 1981 = pretreatment year.
[b] Mean (± SE).

invertebrate activity and foraging signs on herbicide-created snags indicated that birds were using this newly available food resource (McPeek 1985). Berner and Grubb (1985) reported an increase in abundance of some winter bark-foraging bird species when supplemental food was provided ad libitum in an eastern hardwood forest. Blackford (1955) observed a concentration of woodpeckers in a forested area after fire-killed trees became infected with bark-borer beetles.

Live tree availability decreased by 6.4% while snag availability more than doubled on our study area. A numerical response of winter bark-foraging birds to increased snag availability may not have been observed because most species did not depend heavily on snags as feeding substrates, because food was not limiting to bark-foragers, or because they did not feed as heavily on bark-dwelling insects as they did on fruits and seeds (Williams and Batzli 1979). Territoriality of bark-foragers during the breeding season may have contributed to the lack of a numerical response following treatment. By spring 1985, only 4 herbicide-created snags contained cavities excavated by primary cavity-nesters. A numerical response to treatment may occur as snags become more acceptable substrates for bark-foraging cavity-nesters. Van Horne (1983) warned that density may not be a reliable indicator of habitat quality; we did not collect data on reproduction and survival of bark-foragers. Increasing snag availability beyond 15 snags per ha may have increased the fitness of bark-foragers by increasing foraging efficiency, but it did not result in an increase in bird abundance.

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Color dichromatism in female American Redstarts.—Male American Redstarts (*Setophaga ruticilla*) are easily categorized by plumage into yearlings (subadults) and adults. Here we relate differences in plumage and color of females of the species to their age and to the age of their mates. Differences of color in patches of yellow or orange on parts of the body and the tail feathers of female American Redstart have been attributed to age (Chapman 1907, Ficken 1964). As there is a significant difference in the external measurements and weights between first-year and older birds in many species (Crawford and Hohman 1978, Koenig 1980, Norman 1983, Roskraft and Jarvi 1983, Alatalo et al. 1984 and references cited therein), we examined morphological measures as possible indicators of female age. Further support for this approach comes from significant differences between subadult and adult male American Redstarts in wing chord and culmen and tarsus length (Lemon, unpubl. data). Some of our data come from females captured in more than one year, thereby allowing us to assess differences in these individuals over time.

Materials and methods.—We caught females in mist nets, and then banded them during the breeding seasons of 1981–1985. Birds were captured in mixed deciduous-coniferous forests on or near properties of the Huntsman Marine Laboratory, St. Andrews, New Brunswick. The male in the vicinity of the nest or area where a female was captured was assumed to be her mate. No mate could be assigned for 5 females. We made morphological measurements and removed the sixth right rectrix on each bird.

We classified the colors of the yellowish portions of the ventral surface of the wider vane of the sixth right rectrix of 83 females, using the Munsell Book of Color (Anonymous 1976), and following standard techniques of usage (American Society for Testing and Materials 1968). The Munsell system of color notation specifies a given color in terms of three characteristics: hue, value, and chroma. Hue denotes the redness, blueness, etc., of the color; value specifies the greyness; and chroma indicates the intensity. The feathers were placed against the white background supplied with the charts, and were viewed from an angle perpendicular to the specimen. Natural light from a north facing window illuminated the specimen and color plates from an incident angle of 45°. Feathers were assigned to the Munsell color chip to which they were most similar. No attempt was made to interpolate between color chips. The classification of the first author was compared to that made by the last two authors. The results showed only minor discrepancies.

External measurements, including wing chord and culmen and tarsus length, were determined using vernier calipers. We also weighed each bird on a Pesola spring scale. The entire length of the sixth right rectrix, as well as the length of the brown tip of the rectrix, was measured using calipers. The ratio of the length of the brown tip to the total length of the rectrix was calculated to examine the relative extent of the two contrasting colors on a single feather.

A one-way analysis of variance was performed on the morphological data to examine the possibility of any between-year variability due to differences in field technique and personnel. Rather than perform the analyses separately by year, with a consequent reduction in sample size, we used correction factors to permit the combination of data from 1982, 1984, and 1985. The variances of the measurements were not significantly different for these years (Bartlett-Box F-test, $P > 0.10$); therefore, the differences in the means of the two variables significantly different between 1982 and 1984 were used to adjust the 1982 data. For all observations made in 1982, we added 0.1108 to the tarsus length and subtracted 0.0839 from the culmen length.

Principal component analysis was carried out using the PRINCOMP program of the Statistical Analysis System) (Sarle 1982). Discriminant analyses were done using the DISCRIMINANT program of Klecka (1975).

Results.—All feathers appeared pale yellow to the observers. All had a Munsell value of 9, so value was of no use as a discriminator. The feathers were grouped into either of two hues, 5Y which we designate as "yellow," and 2.5Y which we designate as "orange." Feathers were then ranked on individual chromas within each hue (Table 1), with a neutral chroma 1 between the two hues. The frequency distribution so obtained is bimodal, and it is in this sense that we refer to the colors as "dichromatic."

We used three methods to relate these differences in feather color to possible differences in ages of the subjects and to ages of mates. First, we examined morphological differences that we sometimes associated with age. If we hypothesize that the females with the more orange feathers are older than those with more yellow feathers, just as adult males are more orange than subadult males, then we predict that the orange-feathered females should be larger than yellow-feathered females with respect to certain morphological features. In fact, of all measures made, only tarsus length showed a significant mean difference between the two groups (mean tarsus length: orange females, $\bar{x} = 1.93 \pm 0.060$ cm [SD], N = 21; yellow females, $\bar{x} = 1.87 \pm 0.095$ cm, N = 41; $F = 2.5$, df = 1,48, $P < 0.05$). The results of a

TABLE 1

NUMBER OF FEMALE AMERICAN REDSTARTS SORTED BY HUE AND CHROMA ASSIGNED TO THE YELLOWISH PORTION OF THE RIGHT RECTRIX

	Hue					
	"Orange"				"Yellow"	
Chroma[a]	8	6	4	Neutral	4	6
Number	9	11	6		15	42
Totals	26				57	

[a] 4 = low intensity, 6 = moderate intensity, 8 = high intensity.

principal component analysis of the combined morphological data from 1982 and 1984 showed no obvious separation between females with orange or yellow rectrices. Similarly, stepwise discriminant function analysis did not separate the two groups. In conclusion, morphological evidence that orange females are larger, and, therefore, assumed to be older, is limited to differences in tarsus length.

A second basis for examining feather color and age comes from demography. In our study, about 65% of the breeding male American Redstarts are adults. Assuming the proportions are the same for age of females, as is the case in the Prairie Warbler (*Dendroica discolor*) (Nolan 1978), there should be more "orange" than "yellow" females. In fact, the proportions observed were opposite to those predicted (Table 1).

Adult males arrive on breeding grounds about 7 to 10 days earlier than yearling males (Procter-Gray and Holmes 1981). These older males acquire mates before the younger males. Therefore, if older females arrive earlier than do younger females, as they do in White Wagtails (*Motacilla alba*) (Leinonen 1973), then more often older females should pair with adult males than with subadult males. As predicted, a disproportionate number of orange females mated with adult males: of 25 orange females, 23 had adult mates, while of 53 yellow females, 35 had adult mates ($\chi^2 = 6.01$, df = 1, $P < 0.02$).

The third approach of assessing the relationship between color and age is to examine year-to-year color changes of banded females (Table 2). The number of such recaptured individuals was small. Two of 6 females first recorded as yellow changed to orange in a later year; but both then changed from orange back to yellow in a subsequent year. Three individuals remained yellow over two years, and one remained orange. Obviously, color is not strictly related to age.

Discussion.—The use of morphological structures of the females as an indicator of age may be useful in some species, but this is not always the case (Knapton 1978). Furthermore, even measurements with significantly different means may overlap considerably between groups, and consequently may be poor discriminators (Alatalo et al. 1984).

Although Nolan (1978) noted no tendency for either sex to pair preferentially with an age class of the other sex in Prairie Warblers, the distribution of female American Redstarts observed in this study seems to indicate some form of selective mating. In studies of Meadow Buntings (*Emberiza cioides*) (Yamagishi 1981) and Great Tits (*Parus major*) (Greenwood et al. 1979), the smallest percentages of breeding pairs were composed of older females mated

TABLE 2

MUNSELL COLORS ASSIGNED TO THE YELLOWISH PORTIONS OF RECTRICES OF FEMALES RECAPTURED IN DIFFERENT YEARS AND THE AGES OF THEIR MATES

Female	Year	Hue	Chroma[a]	Age of mate[b]
249	1982	Yellow	4	ASY
	1984	Yellow	4	ASY
291	1982	Yellow	6	SY
	1983	Yellow	6	SY
330	1983	Yellow	6	?
	1984	Orange	8	ASY
	1985	Yellow	4	ASY
976	1981	Yellow	6	ASY
	1982	Yellow	6	ASY
478	1984	Orange	4	ASY
	1985	Orange	4	ASY
980	1981	Yellow	6	ASY
	1983	Orange	4	ASY
	1985	Yellow	6	ASY

[a] 4 = low intensity, 6 = moderate intensity, 8 = high intensity.
[b] SY = subadult; ASY = adult; ? = age unknown.

to younger males (2.6% in the former study, 16% in the latter). Pigmentation may also be related to diet and condition. Chemical analysis of feathers of wild finches revealed that the difference between orange and yellow birds was an apparent buildup of dietary carotenoid (Brush and Power 1976). Since all our banded females did not change color from year to year in a manner consistent with age, it is possible that differences in female color are partly a reflection of diet, as well as age, and that females with certain feeding backgrounds arrive earlier.

Dwight (1900) and Wood (1969) stated that the main molts of American Redstarts occur in July and August for juveniles of the year, followed in each succeeding year by a molt in March and April, chiefly on the head and throat, and a complete postbreeding molt in July and August. Problems in color analysis may arise if feathers are taken at different times during the season. The plumage color of House Finches (*Carpodacus mexicanus*) changes without a molt, due to abrasion and wear in a single feather generation (Michener and Michener 1931, as cited by Brush and Power 1976). Although this should not affect the assessment of Munsell hue, it may increase the Munsell chroma as greyish feather edges are worn away (Brush and Power 1976), and it should be considered if chroma is to be included in an aging technique.

Summary.—We attempted to determine whether color or morphological characters of female American Redstarts could be used as indicators of age. Tail feather patches fell into two categories of orange or yellow. Orange females had longer tarsi and mated disproportionately with older males; however, orange females were proportionately less frequent in the population than expected if all two-year-old or more females were "orange." Tracking histories of females showed that they do not consistently change from yellow to orange with age, and that some change from orange to yellow.

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Nest-site quality and reproductive success of early- and late-nesting Double-crested Cormorants.—Reproductive success of some colonially breeding waterbirds can differ in nests positioned centrally or peripherally in a colony (see Knopf 1979 for review), the relative timing of breeding, and the age or experience of breeders (Dexheimer and Southern 1974, Ryder 1975, Blus and Keahey 1978, Blomme 1979, Hogan 1979, Knopf 1979, Potts et al. 1980, Parsons and Burger 1981, Ryder and Ryder 1981, DesGranges 1982, Debout 1985, Shaw 1986). In many species of cormorants and other colonial waterbirds, birds arriving at the colony early in the breeding season have bred before, and they select the best available nesting sites, often older nest foundations (McLeod and Bondar 1953, Blomme 1979). These early breeders generally nest in the colony center and raise the most young.

Little is known about the effects of nest-site quality in tree-nesting colonial waterbirds except that the clutch size in one colony of Double-crested Cormorants (*Phalacrocorax auritus*) increased with increased nest height (Blomme 1979). Factors important for ground-nesting cormorants such as the amount of exposure to rain (Potts et al. 1980) and ease of defense against intraspecific nest thieves and interspecific predators are probably important to tree-nesting species as well (Tenaza 1971, Potts et al. 1980). The nest-site quality for tree-nesters is presumably related to the strength of trees, which must be strong enough to withstand high winds and prevent the nest or chicks from being dislodged and lost. The aim of the study reported here was to determine whether the reproductive success of early and late nesting Double-crested Cormorants varied with the health and strength of the nest trees or their use as nest-sites during the preceding breeding season.

Study area and methods.—Observations were made at a colony of 1940 pairs of Double-crested Cormorants on Ile aux Loups Marins, an island of the Iles de la Madeleine Archipelago in the Gulf of St. Lawrence between 47°13′ and 47°39′N, and 61°23′ and 62°01′W. This 14-ha island is covered with 5–7 m tall conifers (*Abies balsamea* and *Picea glauca*) in which cormorants and Great Blue Herons (*Ardea herodias*) nest. Great Black-backed (*Larus marinus*) and Herring (*L. argentatus*) gulls also breed on the island (Léger 1984, Léger and McNeil 1986).

The trees used as nesting sites were checked for the presence of active nests every 5–6 days between 6 and 31 May 1980, and progressively less frequently until mid-July. Nest-building extended from the end of April to mid-July; 54% of the nests were built before mid-May, 19% in the second half of May, 15% in June, and 11% in July (Léger and McNeil 1986). Trees with nests were classified as (1) healthy (full of green needles), (2) morbid (needles beginning to fall), (3) dead (solid trees without needles), or (4) rotten or broken trees. The strength of the trees was judged "bad," "good," or "excellent," depending on their resistance to a lateral push. Observations by Burton (1978) and Pilon et al. (1983) permitted us to determine whether trees had been used for nesting during previous years. Nest contents were checked using a mirror fixed to the end of a 6-m metal pole.

The relationship between observed frequencies of early and late nests as a function of nest-site characteristics was examined using two-way contingency analyses (Nie et al. 1975, Legendre and Legendre 1983). Variables were divided into discrete classes using the PARTI program within the R package (Centre de calculs, Université de Montréal). The success of early and late nests was compared using tests of significance of percentages (Lamotte 1971) and *t*-tests for comparing mean values (Sokal and Rohlf 1981).

Results.—From 6 May to mid-July 1980, 89 nests were checked. There were 50 nests of early breeders (established in early May), all in the center of the area occupied by the colony, and 39 nests of late breeders (June), all on the fringe of the colony, near breeding gulls. Late nesting cormorants built nests close to breeding gulls, and, when we visited the colony, the

TABLE 1
REPRODUCTIVE SUCCESS OF EARLY AND LATE NESTING DOUBLE-CRESTED CORMORANTS

	Early breeders (6–14 May)	Late breeders (June)
Mean number of eggs per nest	3.32 ± 0.09 (50)[a]	2.74 ± 0.88 (39)
Mean number of fledglings per successful brood	2.80 ± 1.10 (45)	1.87 ± 0.09 (30)
Mean number of fledglings per initiated clutch	2.59 ± 1.27 (49)[b]	1.41 ± 1.14 (39)
Percent of initiated clutches with fledged young	93.9	74.4
Percent of eggs that produced fledged young	68.6	51.4
Percent of eggs which produced fledged young from successful broods	72.0	67.0

[a] $\bar{x}$ ± SD (number of nests).
[b] The number of young in one of the 50 nests is unknown.

former flew away in greater numbers and for longer periods than did the early nesting birds in the center of the colony.

Reproductive success.—We define a clutch as "successful" if at least one young fledged, and a brood as "initiated" if at least one egg was laid. The mean clutch size, the mean number of fledglings per initiated brood and per successful brood (all t-tests, $P < 0.05$), the percentage of initiated clutches, and the percentage of eggs producing fledged young in initiated clutches (all tests of significance of percentages, $P < 0.05$) were significantly higher in early breeders (Table 1). Late nesting pairs abandoned proportionally more nests (9 out of 39) than did early breeders (3 out of 50). In successful broods, the percentage of eggs producing fledged young did not differ between early and late nesters ($P < 0.05$).

Nest-site quality.—When we considered all the nests built on Ile aux Loups Marins in 1980 (unfortunately we do not have data on their reproductive success), the values of the Wilks χ^2 calculated in the contingency analysis indicated that the health and strength of nest-bearing trees and their use as nest-sites in previous year(s) significantly discriminate between the early nests and late nests for which the reproductive success was observed (Table 2). More early nesters (May) used previously used nest sites than did late nesters (June and July), and proportionally more late nests than early nests were supported by healthy trees of excellent strength that were not used for nest-support during previous years. If we take the asymmetric uncertainty coefficient into account, however, previous use of trees accounts for the greater proportion of variation.

Discussion.—Our data on the reproductive success of early and late nesting Double-crested Cormorants agree with those obtained by Ellison and Cleary (1978), Blus and Keahey (1978), Knopf (1979), Hogan (1979), and Potts et al. (1980), who found that late breeding pelecaniform birds were usually younger, less experienced, and less persistent incubators and less successful in catching fish than were early breeders. Their nests were often left unattended and were thus more exposed to intraspecific actions of other breeders as well as to predation. At Ile aux Loups Marins, late nesting Double-crested Cormorants laid fewer eggs (1 to 4) than did early breeders (2 to 6), and they lost more eggs and nestlings. Similarly, late nesting Brown Pelicans laid fewer eggs and lost more young (Blus and Keahey 1978).

The proportionately greater nest abandonment in late nesting Double-crested Cormorants

TABLE 2

CONTINGENCY ANALYSIS OF VARIATION IN SITE QUALITY OF NESTS BUILT BY DOUBLE-CRESTED CORMORANTS IN DIFFERENT PERIODS IN 1980

Nest-site quality variable	χ^2 (Wilks)	Asymmetric uncertainty coefficient	Partitions	Periods			
				6–14 May	20–25 May	June	July
Formerly used trees	407.52[a]	0.120	Yes	583 (**0.72**)[b]	167 (**0.21**)	49 (0.06)	11 (0.01)
			No	193 (0.30)	120 (0.19)	171 (**0.27**)	151 (**0.24**)
Health of the trees	380.36[a]	0.110	Healthy	27 (0.12)	30 (0.13)	93 (**0.40**)	85 (**0.36**)
			Sick	54 (0.40)	29 (**0.22**)	27 (**0.20**)	25 (**0.19**)
			Rotten or broken	695 (**0.65**)	227 (**0.21**)	101 (0.09)	52 (0.05)
Strength of the trees	17.80[a]	0.005	Excellent	335 (0.52)	98 (0.16)	111 (**0.18**)	83 (**0.13**)
			Good or bad	439 (**0.54**)	187 (**0.23**)	110 (0.14)	79 (0.10)
Unconditional probability				0.53	0.20	0.15	0.11

[a] $P < 0.001$.

[b] Values in parentheses represent the conditional probability. The conditional probabilities which exceed the corresponding unconditional probabilities are in bold-face type.

on Ile aux Loups Marins (see also Siegel-Causey and Hunt 1986) could have been due to egg or nestling predation as a result of human disturbance (Ellison and Cleary 1978, DesGranges and Reed 1981). Excluding abandoned nests, the percentage of eggs laid by late breeders that produced fledged young did not differ significantly from that of early breeders (Table 1). Similar data were reported by Knopf (1979) who found that lower reproductive success in late breeding White Pelicans was largely due to a higher frequency of nest abandonment.

The majority of the late nests in this study were in healthier trees than early nests. The strength of a higher proportion of these trees with late nests was also judged excellent (Table 2).

Little is known of nest-site quality of peripheral late breeders of any species. In ground-nesting Shags (*Phalacrocorax aristotelis*), Potts et al. (1980) found that the youngest birds bred on poor sites and had lower reproductive success, but the reproductive success of late breeders remained lower than that of early breeders on sites of equal or comparable quality. According to Blomme (1979), the reproductive success of Double-crested Cormorants increased with increasing nest height, but was not affected by nest size. DesGranges (1982), on the other hand, found that experienced adults built larger nests and reared the most young to fledging. The chances that eggs and young could be dislodged from the nest should decrease with nest size, but we do not have any data to test this. For tree-nesting cormorants in a windy region such as Iles de la Madeleine, however, nest stability should involve trees that are strong enough to withstand high winds. On a day of very high winds (up to 117 km/h) in 1979, 85 out of 1289 nests of Double-crested Cormorants were dislodged on Ile aux Loups Marins; most of them were in areas where trees were dead, rotten or broken, and pertained to early nesters (Léger 1984).

Siegel-Causey and Hunt (1986) found that first arrivals at a colony of ground-nesting Double-crested Cormorants selected existing nests over all other possibilities; site fidelity did not appear to be important. Among all the nests built on Ile aux Loups Marins in 1980, those built first were supported by trees in poorer condition than trees supporting later nests (Table 2 and Léger 1984). This suggests that early nesters selected trees that had been used in previous years, even if stronger (but unused) trees were available. Unfortunately, we do not have any data on the age of nesters. Taking into account the findings of McLeod and Bondar (1953) and Blomme (1979), however, we suggest that early arriving and early breeding cormorants were older, experienced, nesters that built their nests in preferred sites on previous years' foundations. Early nesters probably continue to use the same sites year after year until the tree is too weak to support their nest. The same tree may be occupied until a nest is lost due to wind action or because the tree has fallen. Early nesters may then renest on healthy or less damaged trees on the fringe of the area occupied by the colony, depending on the time in the breeding season. We also suggest that younger individuals breeding for the first time built nests on the fringes of the colony and laid later. Trees in this zone had been used for nest-support for the first time or had been used only fairly recently and were thus less damaged as a result of the direct and indirect effects of bird excrement on the vegetation.

Conclusion.—Many late nesting Double-crested Cormorants, despite being in relatively stronger trees, had a lower reproductive success than did early nesters. We eliminate tree condition as an operative factor in nesting success. What did cause nesting success of late and fringe-nesters to decline is unknown.

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High basal metabolic rate in Sanderlings (*Calidris alba*).—Physiological data from a number of species permit the estimation of basal metabolic rate (BMR) from allometric equations (Lasiewski and Dawson 1967, Aschoff and Pohl 1970, Kendeigh et al. 1977). Here I report BMR for Sanderlings (*Calidris alba*) taken on their wintering grounds on the Peruvian Coast and compare these results with estimates of BMR from three allometric equations.

Methods.—Nine Sanderlings (all adults, sex unknown) were caught with mist nets on Villa beach, near Lima, Peru, on 21 August 1984 at 22:00. They were kept in the laboratory over night at 19°C. BMR for each bird was measured the next day beginning at 8:00. BMR was estimated from oxygen consumption of the birds during 30-min periods. All individuals were in a postabsorptive (without food in their stomachs) condition, and they had been resting in a dark 1-l metabolic chamber for at least 1 h prior to the experiments. The temperature in all the determinations was 25 ± 1°C [SD] (see Castro et al. 1985).

I tested the accuracy of the apparatus by measuring oxygen consumption in a strain of laboratory mice of known basal metabolism. The results fitted the expected values.

Results.—Mean body weight was 50.44 ± 4.59 g [SD]. Mean oxygen consumption was 1.98 ml/g/h ± 0.53, equivalent to 48.15 kJ/day assuming a conversion factor of 20.1 kJ per liter of oxygen consumed (fat and carbohydrate metabolism, Dawson 1974).

These results are 12–28% higher than those predicted by the equations of Aschoff and Pohl (1970), Lasiewski and Dawson (1967), and Kendeigh et al. (1977) (Table 1).

Discussion.—Few measurements of shorebird BMR have been published. Thus it is difficult to know whether the high values reported here might be representative of shorebirds in general. Johnston and McFarlane (1967) showed values for 2 individuals of the Lesser Golden-Plover (*Pluvialis dominica*). One of them had a value 14% lower than that predicted using Aschoff and Pohl's (1970) equation, but the other had a value 28% higher than predicted. Johnston and McFarlane rejected the second measurement, arguing that the bird in question "evidently never reached a basal level" based on allometric predictions. Kendeigh et al. (1977) reported a value for *Charadrius dubius* that was 34% higher than that predicted by Aschoff and Pohl (1970). Kersten and Piersma (in press) report values for three other species of shorebirds that run an average of 34% over those predicted by Aschoff and Pohl's (1970) equations. Thus it appears likely that shorebirds have higher metabolic rates than

TABLE 1
COMPARISON OF THE VALUES OF BMR WITH THE PREDICTED VALUES FOR A 50-G SANDERLING

	Metabolism (kJ/day)	Difference from actual measurement
Actual measurement	48.13	
Allometric equations		
Aschoff and Pohl[a]	42.84	+12%
Lasiewski and Dawson[b]	37.53	+28%
Kendeigh et al.[c]	38.70	+24%

[a] Nonpasserines in the diurnal cycle.
[b] Nonpasserines, day and night.
[c] Eq. 5.5 (nonpasserines, day and night).

those predicted from standard allometric equations. Passeriformes also show higher BMR than predicted by the above allometric equations; however, the adaptive value of a high BMR is unclear (see Kersten and Piersma [in press] for further discussion).

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On the antipredator advantages of coloniality: a word of caution.—The possible antipredator advantages of coloniality in many species of waterbirds are discussed in recent papers on the evolution of mixed-species colonies (Burger 1981) and the adaptive significance of coloniality (Wittenberger and Hunt 1985). Possible advantages include early warning, mobbing, and predator "swamping" via breeding synchrony. While I agree that conspecific and heterospecific signals can alert other colony members to the presence of a predator, not all species or mixed species groups give such signals. For example, there is no strong evidence that ciconiiforms mob predators. Also, based on my studies of ciconiiforms, I believe predator "swamping" via breeding synchrony may be overestimated in reducing predation. Here I present examples of coloniality affording no protection from predation.

In 1981, the Pleasant Grove colony (Hillsborough County, Florida) contained: 75 nests of Anhingas (*Anhinga anhinga*), 225 nests of Wood Storks (*Mycteria americana*), 250 nests of Cattle Egrets (*Bubulcus ibis*), and 30–40 nests of other species of herons. The colony covered ca 2.4 ha of a 9.4-ha phosphate mine impoundment dominated by willow (*Salix caroliniana*), which was the primary nesting substrate. Because of a washout of an earthen dike during heavy rains in May 1979, water at the site did not accumulate in the impoundment as in previous years. By the beginning of the breeding season in late March 1981, the water depth ranged from 15 to 30 cm. In late April, as the colony neared what would be the peak of egg hatching, the water level was low enough to expose the soft mud bottom and large numbers of fallen trees and limbs. At this time, raccoons (*Procyon lotor*) began to prey on the eggs and hatchlings of all species. By 13 May all nests were preyed upon or abandoned. No adult mortality was detected. In subsequent years (1982–1986), the water levels have reached a depth of 15–30 cm (similar to the 1981 season), but colony members have not returned to breed at the site.

Another less dramatic example of predation of Wood Stork nests occurred at the NE Mulberry colony (Polk County) in 1981. At this deep-water phosphate mine impoundment, eggs and nestlings in 24 of 131 stork nests were eaten by raccoons that crossed to three small islands via water hyacinth (*Eichhornia crassipes*).

Though it may be argued that the adults escaped predation to nest another year, the >550-nest Pleasant Grove mixed waterbird colony did not "swamp" raccoon predation. It appears that wading bird colonies of this size do not necessarily afford protection from mammalian predators in all instances (Lopinot 1951, Emlen et al. 1966, Burger 1974, Southern et al. 1985). Even avian predators can cause large scale nest loss and abandonment (Collins 1970, Hunter and Morris 1976, Burger 1977). Baker (1940) reported heavy predation by less than 40 Common Crows (*Corvus brachyrhynchos*) that destroyed a 4500-nest colony of Little Blue Herons (*Egretta caerulea*) and Snowy Egrets (*E. thula*) in less than a month.

The proposed advantages of wading birds nesting colonially are many (see review in Burger 1981, Wittenberger and Hunt 1985), and include mate location (especially in species with short-range courtship signals; Rodgers 1980); food resource information (see Krebs 1974, Burger 1981, and citations therein); defense afforded by group action (e.g., Kruuk 1964, Montevecchi 1977); and the Darling effect of stimulation of reproductive activity by the presence and activity of other colony members (Darling 1938, Gochfeld 1980, and citations therein). However, I believe colonial breeding also incurs a disadvantage, as the colony is highly obvious via auditory (calls of adults and young), olfactory (birds, guano, and dropped food items), and visual (large, often light colored species flying in and out of the site) cues to predators. Colonial breeding also can result in intraspecific and interspecific competition for nest sites (Burger 1978) and food resources (Hunt et al. 1986). In addition, the mixed-species wading bird colonies I have studied in the southeast United States appear

to exhibit less total colony synchrony than is reported for other species of nesting birds (e.g., Burger 1978, Gochfeld 1980). For example, Great Blue Herons (*Ardea herodias*) and Anhingas usually begin breeding well in advance of other species of ardeids and the ultimate effect is a protracted breeding season in which the colony becomes less synchronous and any potential "swamping" effect is reduced. To compensate for the increased susceptibility to predation and still gain the advantages of coloniality, colonial nesters generally breed in inaccessible locations, such as on islands and in marsh and swamp vegetation over water (Lack 1968). But once a colony is accessed by the predator, the results may be drastic.

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The foraging behavior of Gray Gulls at a sandy beach.—The Gray Gull (*Larus modestus*) is a medium-sized gull restricted to western South America, where it breeds inland at barren nitrate deserts and feeds along the coast (Johnson 1965, Howell et al. 1974). Foraging occurs in two distinct habitats: at sea, where fish and crustaceans are captured by surface seizing (Chapman 1973, Howell et al. 1974, Duffy 1983); and at sandy beaches, where foraging for the crustacean *Emerita analoga* occurs in the wave-washed zone (Murphy 1936, Johnson 1965, Howell et al. 1974). The foraging behavior of Gray Gulls at sea has been described (Duffy 1980, 1983), but nothing is reported of their foraging behavior on sandy beaches, other than the habit of running up and down in the wave-washed zone like sandpipers, probing at air bubbles left by *Emerita* (Murphy 1936, Johnson 1965, Howell et al. 1974). This study describes the foraging behavior of adult and immature Gray Gulls at a sandy beach in central Chile.

Study area and methods.—We observed Gray Gulls foraging on a fine-grained sandy beach south of Las Cruces (33°30′S, 71°38′W), central Chile, for four tidal cycles during October and November 1985. The beach supported many *Emerita analoga,* evidenced by sieved samples at low tide. Wave action was high throughout, and a moderate to strong onshore wind blew during most observation periods. Birds were aged as adult or immature on the basis of plumage characteristics (Harrison 1983).

We recorded (1) search time—the time (measured to the nearest sec) between picking or probing attempts by birds foraging in the wave-washed zone, (2) the type of feeding attempt made (see below), (3) the proportion of successful feeding attempts, (4) the fate of prey items, and (5) the handling time between prey capture and swallowing. A successful attempt was one in which a prey item was captured, although not necessarily swallowed. Two distinct foraging techniques were recognized: (1) picking prey that were on or just below the surface with the tip of the bill, and (2) probing into the sand for prey with the mandibles slightly apart. Picking was subdivided into "dry" picking, where prey were taken from wet sand or water shallower than bill length; and plunging, where prey were taken from water deeper than bill length. The sizes of prey items eaten by Gray Gulls were estimated as a proportion of bill length.

Results.—No Gray Gull was present at the beach until 90 min before low tide, and all departed within 120 min after low tide. At other times birds either went out to sea or roosted at rocky headlands. Foraging birds occurred singly or in small flocks of up to 15 individuals. Gray Gulls either ran or flew down the beach as the waves receded. Running predominated where the beach was steep and the distance from the region above the edge of the wave-washed zone to the foraging area was ≤ 15 m. Where the beach was broad and shallow, birds tended to wait for times when the waves receded up to 50 m, which occurred once every 5 to 10 min. The Gray Gulls would then fly out to the foraging area and capture prey,

TABLE 1
THE PROPORTIONS, FREQUENCIES OF SUCCESS, AND RATES OF DIFFERENT FORAGING TECHNIQUES USED BY GRAY GULLS FEEDING AT SANDY BEACHES

Foraging technique	% attempts (N)	% success	Time between attempts (sec)
Picking	47.0 (101)	50.5	16.8 ± 12.9 (101)[a]
Dry picking	37.2 (80)	53.8	13.8 ± 11.3 (80)
Plunging	9.8 (21)	38.1	28.6 ± 12.1 (21)
Probing	53.0 (114)	12.3	15.9 ± 9.2 (58)

[a] Mean ± SD (N).

either by picking them up while flying, or by landing and probing. Flying birds fed by picking significantly more frequently (88.8%, N = 80) than did walking birds (28.0%, N = 100) ($\chi^2 = 66.27$, df = 1, $P < 0.001$).

Picking was successful more frequently than was probing ($\chi^2 = 37.01$, $P < 0.001$) (Table 1), although the differences in success rate between dry picking and plunging, and between plunging and probing were not significant ($\chi^2 = 1.64, 2.38$, $P > 0.1$). Immatures did not forage by plunging (N = 82 attempts), but rather they foraged primarily by probing (95% of attempts), whereas adults foraged primarily by picking (73% of 135 attempts).

The foraging rate of adults and immatures combined, as indicated by the mean interval between foraging attempts, varied with different foraging techniques (ANOVA, $F = 16.08$, df = 2, 132, $P < 0.001$) (Table 1). The foraging rate of adults alone, however, was not different between dry picking and probing, but both were significantly higher than the rate for plunging birds (Newman-Keuls test).

All prey eaten appeared to be *Emerita,* although some of the smaller prey items may have been isopods (*Cirolana* sp.), which were abundant in the area. Prey size ranged between 0.2 and 1.0 × bill length (mean 0.52 × bill length, N = 26). The mean prey handling time of adults (1.2 ± 3.3 sec [SD], N = 57) was shorter than that of immatures (24.5 ± 22.4 sec, N = 6). Of the eight prey items caught by immatures, one was lost when it was dropped in the sea, and one was stolen by another immature Gray Gull. Two attempts at intraspecific prey robbery were observed, both involving immature gulls. No adults lost prey items or were robbed by other birds. An adult Gray Gull twice attempted unsuccessfully to rob a Sanderling (*Calidris alba*) struggling with a large *Emerita,* by flying at and chasing the Sanderling.

Assuming a mean handling time of 3.4 sec, gulls caught 1.88 prey/min when dry picking, 0.71 prey/min when plunging, and 0.38 prey/min when probing.

Discussion.—Gray Gull foraging periodicity on sandy beaches is limited by the tidal cycle, presumably as a result of the distribution of prey on the shore. Foraging while walking apparently is preferred to foraging while flying (Murphy 1936, Johnson 1965, Howell et al. 1974, this study), presumably because walking is less costly energetically than is flying. The cost of foraging by flying is at least partly offset by an increased energy intake rate as a result of a high proportion of foraging by picking, the most time efficient prey capture technique, during aerial foraging.

The limited data presented here suggest that immature Gray Gulls are less efficient foragers than are adults, as is typical of many gull species (e.g., Verbeek 1977, Searcy 1978).

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Internest displacement of White Ibis eggs.—During a study of nesting success at a White Ibis (*Eudocimus albus*) colony (Shields and Parnell 1986), I observed five cases in which an egg laid in one nest was subsequently found in another nest in the same tree or shrub. The study was conducted during the 1983 and 1984 breeding seasons at Battery Island, North Carolina (33°54′N, 78°01′W), where White Ibises nested in a maritime shrub thicket (see Shields and Parnell 1986 for a complete description of the area). I marked 694 eggs in 1983, and 1213 eggs in 1984, with unique alpha-numeric codes. I visited nests 1–3 times per week from the onset of egglaying through hatching to record fates of eggs. I ruled out the possibility that I may have accidentally placed eggs in the wrong nests after marking them. I temporarily removed eggs from a nest for marking only on the date I first observed the eggs. Internest displacement of four eggs occurred several days after they were marked, and one case involved an unmarked egg.

I detected two instances of internest displacement of eggs in 1983, one involving a marked egg and one an unmarked egg. On 16 April, nests 96 and 97 contained three eggs each. On 21 April, nest 97 held three eggs, while only two eggs were present in nest 96; the third egg was found on the ground with one side punctured in the manner characteristic of crow predation (Rearden 1951). Fish Crows (*Corvus ossifragus*) were common in the colony, and crow predation on ibis eggs was high (Shields and Parnell 1986). On 28 April, I found another egg from 96 on the ground with a hole in its side; the remaining egg, which was slightly cracked, was discovered in nest 97. All four eggs in 97 hatched between 3–10 May.

Nest 59 held two eggs on 13 April and four eggs on 16, 21, and 28 April. On 3 May, the first egg had begun hatching, and a fifth egg was present. Three days later the nest held four chicks and one of the original four eggs, which hatched between 6–10 May. Because the

fifth egg was present in nest 59 no more than nine days prior to hatching, and because incubation in the White Ibis requires 21 days (Rudegeair 1975, Kushlan 1977), it could not have been laid in nest 59. Ibis nesting within a given tree or shrub was synchronous in 1983 (pers. obs.). Because the fifth egg was at approximately the same stage of incubation as the eggs in nest 59, it may have been displaced from one of the 5–10 unmarked nests in the same shrub.

Three cases of egg displacement in 1984 involved marked eggs. Nests 52 and 60 contained two eggs each on 11 April. Four days later, nest 52 held three eggs, while nest 60 contained two new eggs only. On 18 April, only two eggs were present in nest 52, and nest 60 contained its two eggs plus one egg from 52, which was cracked and dented. Both eggs in nest 52 subsequently hatched, but nest 60 failed.

On 15 April, nest 67 contained three eggs, and nest 135 contained two eggs. Three days later, I found one egg from 135 in nest 67 and the other on the ground with one side punctured. The four eggs in 67 were depredated by crows a week later.

Nests 91 and 92 held two eggs each on 15 and 18 April. On 25 April nest 92 was empty and one of its eggs was found in nest 91. All three eggs in 91 eventually hatched.

How were eggs displaced from one nest to another? I do not believe that eggs fell from donor to recipient nests (cf. Cannell and Harrington 1984) because of the relative positions of nests. Although nests 52 and 135 were 0.6 m and 0.4 m above the nests to which their eggs were displaced, lateral distances between donor and recipient nests were 0.3 and 0.2 m, respectively. Nest 92 was 0.1 m lower than and 0.5 m away from the nest to which its egg was displaced. I did not measure the distance between nests 96 and 97 in 1983.

Ibises may have moved eggs themselves, as has been reported in the Little Blue Heron (*Egretta caerulea*) (Rodgers 1978). It is unlikely, however, that owners of recipient nests would have intentionally added a foreign egg to their nests. Such behavior would not increase fitness of the recipient birds, and it would in fact reduce their fitness if they invested in a chick not their own at the expense of one or more of their own offspring. Owners of the donor nests, on the other hand, may increase their fitness by moving eggs to other nests (see Trost and Webb 1986). Brood reduction in the White Ibis, however, is severe (Kushlan 1977, Allen-Grimes 1982), and this type of brood parasitism would be a risky strategy, even though ibises apparently do not reject foreign eggs. Relocation of eggs may be an adaptive response to human disturbance of nests (Rodgers 1978, Trost and Webb 1986). If this were the case in the present study, ibises should not have moved their eggs to nests in the same tree or shrub, which were subject to the same level of investigator disturbance as the donor nests. Furthermore, my activities regularly disturbed large numbers of nesting ibises, yet internest displacement of eggs was apparently a very rare event.

During >150 h of general observation in the colony, I never observed ibises carrying eggs. I frequently saw Fish Crows, however, carrying off intact ibis eggs between their mandibles. In three of the four cases of displacement involving marked eggs, the appearance of an egg in the recipient nest coincided with the disappearance or depredation by crows of another egg in the donor nest. Crows typically carry off whole eggs and eat or cache them. They then return to the same nest to remove additional eggs (Tinbergen et al. 1967, Croze 1970, Montevecchi 1976). Fish Crows may have dropped or placed eggs in other ibis nests during aborted predation attempts.

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Distribution and status of Brown Pelicans in Venezuela in 1983.—The breeding distribution of the Brown Pelican (*Pelecanus occidentalis*) in the eastern portions of its range extends from North Carolina through the Gulf of Mexico and Caribbean to eastern Venezuela (Palmer 1962). Few data exist on locations and sizes of nesting colonies in the Caribbean region, especially in South America (van Halewyn and Norton 1984). Here we present such data for Venezuela.

One of us (HMG) surveyed the 2900-km coastline of Venezuela from Punta Castillete (11°51′N, 71°19′W) to Punta Playa (8°33′N, 60°00′W) and island regions (except Los Monjes, La Orchila, and Aves) from a fixed-wing aircraft (Cessna 170) flying at 100–300 m, and at speeds of 120–160 km/h, in January–February 1983. The flight path paralleled the coastline at approximately 0.1 km offshore and required 44 h. All sightings of birds and nesting colonies were recorded, and the total number of nests in each colony was estimated from near-vertical color photographs taken with a 35-mm camera and 50-mm lens. Numbers of isolated pelicans, whether flying or resting, were counted directly or from photographs.

Pelicans breed in Venezuela between November and June (Guzman, unpubl. data), a chronology similar to breeding pelicans in Florida (Schreiber 1980a). January–February is the peak of nesting, and our surveys thus show the distribution of present colonies. The total

TABLE 1

BREEDING LOCATIONS OF BROWN PELICANS IN VENEZUELA, JANUARY–FEBRUARY 1983

State	Map location	Specific locality	Habitat	Number of nests counted	Number of birds counted resting/ flying by state
Zulia	1	Lagunetas	Mangrove	24	0/81
Falcon	2	Maraguey	Mangrove	307	1387/138
Miranda	3	Carenero	Mangrove	412	0/349
Miranda	4	Buche	Mangrove	87	—
Miranda	5	Tacarigua	Mangrove	235	—
Anzoategui	6	I. Chimanas	Thorn woodland	35	0/328
N. Esparta	7	Las Maritas	Mangrove	291	347/743
D. Amacuro	8	C. Macareo	Mangrove	69	220/0
Los Roques	9	I. Larga	Mangrove	135	0/37
Los Roques	10	I. Canquises	Mangrove	207	—
Los Roques	11	I. Seleskey	Mangrove	43	—
Sucre	1	Chiguana	Mangrove	67	1133/261
Sucre	2	Chacopata	Mangrove	429	—
Sucre	3	La Esmeralda	Humid forest	113	—
Sucre	4	El Diablo	Humid forest	37	—
Sucre	5	Pto. Santo	Humid forest	133	—
Sucre	6	Morro Santo	Humid forest	16	—
Sucre	7	Mala Pascua	Humid forest	167	—
Sucre	8	Las Galdonas	Humid forest	21	—
Sucre	9	Tres Puntas	Humid forest	39	—
Sucre	10	Pica Pica	Humid forest	55	—
Sucre	11	Mejillones	Humid forest	71	—
Sucre	12	Uquire	Humid forest	97	—
Sucre	13	Irapa	Mangrove	210	—
Sucre	14	C. Guariquen	Mangrove	69	—
Dto. Federal	—	—	—	—	0/59
Monagas	—	—	—	—	1425/35
Aragua	—	—	—	—	0/27
La Tortuga	—	—	—	—	0/30
Blanquilla	—	—	—	—	0/25
Testigos	—	—	—	—	0/17
Las Aves	—	—	—	—	9/23

number of nests counted, however, should be considered only as an estimate of the breeding population, as considerable asynchrony in nesting exists (Guzman, unpubl. data; Schreiber 1979).

Distribution and habitat.—Birds nested on the tops of trees, both on islands and the shores of the continent. Nests were sighted in mangroves (*Avicennia germinans* and *Rhizophora mangle*; 2585 nests, 77%), in tropical thorn woodlands (*Plumeria* sp., *Bursera* sp., and *Caparis* sp.; 35 nests, 1%), and in humid forests along the abrupt eastern coast of the country (749 nests, 22%). Twenty-one of 25 colonies were on the continent (along 2519 km of shoreline); 4 were on islands (467 km of shoreline) (Table 1) (Fig. 1). More than half of the

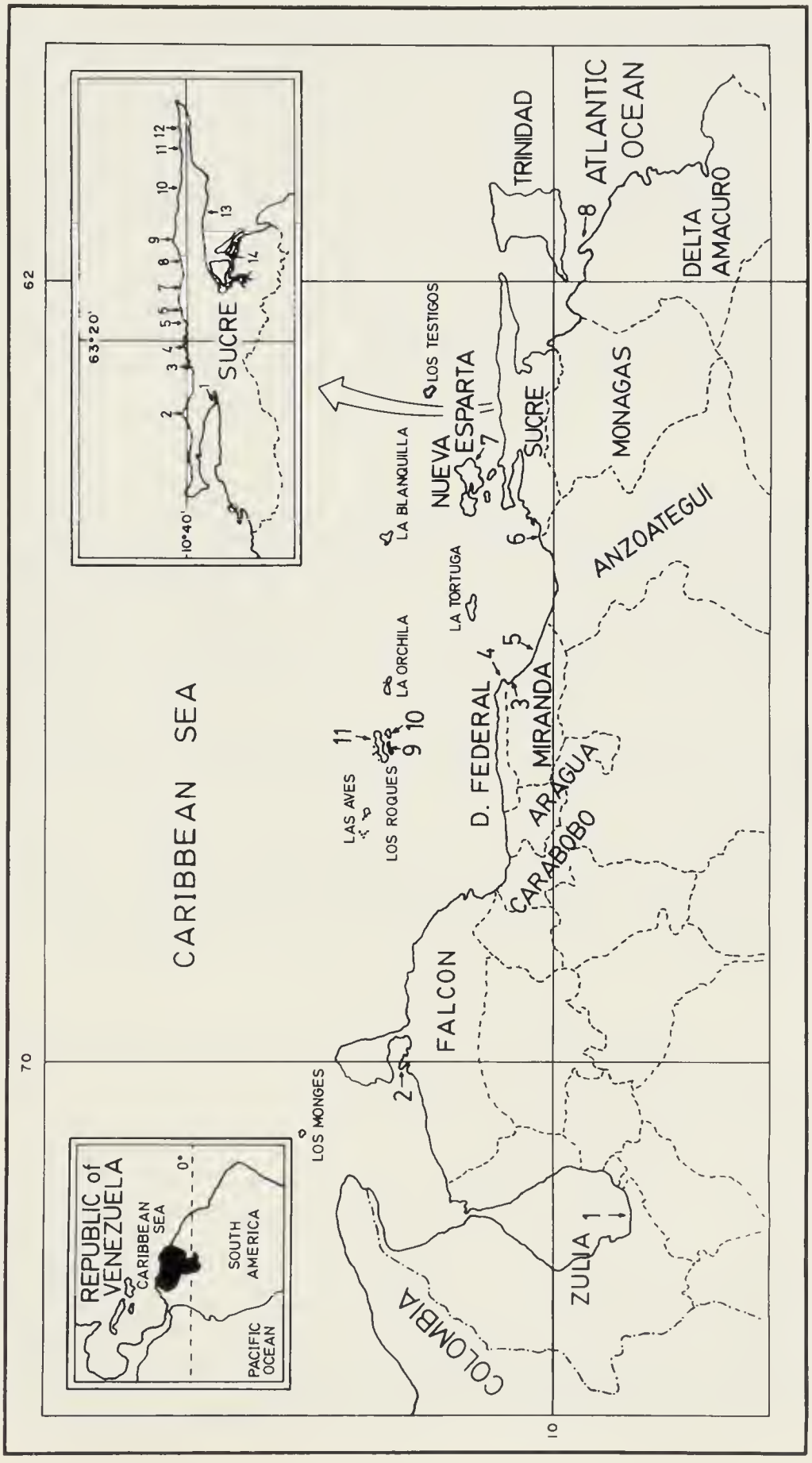

FIG. 1. Locations of Brown Pelican colonies in Venezuela, 1983. Each arrow represents one colony.

colonies were in the state of Sucre, which has the longest coast (705 km), of which almost 70% is escarpment. Most pelican colonies were higher than 40 m above sea level, or in isolated mangrove areas. In western Venezuela, the state of Zulia (225 km shoreline) appears to have considerable habitat for nesting (extensive mangroves bordering Lake Maracaibo); however, only one small colony was found in the area. Although local fishermen said that breeding colonies thrive in the mangroves of Tucacas (state of Falcon), we found none during this survey. Other important colonies exist in the mangroves of Carenero and Tacarigua in the state of Miranda. Although Cory (1909) and Van Der Werf et al. (1958) found breeding colonies in La Tortuga and Las Aves respectively, we sighted none there or on other islands, except for three colonies on Los Roques and one on Margarita (state of Nueva Esparta).

Population size.—A total of 3369 nests were counted (Table 1), along with 6674 individual birds away from colonies. Most birds not associated with nesting colonies were found in large groups on sand spits, primarily in Falcon and Sucre, and in the Delta Amacuro at low tide. In other states, most birds were resting on rocks, in marinas, or in mangroves. We estimated the total population during this study at 17,500 pelicans: 14,000 adults and 3500 juveniles.

Current status.—We have no direct evidence of disturbance to any breeding colony. The possibility, however, exists of indirect effects from habitat changes caused by human recreational activities and urban development, especially in Miranda. The Zulia region has experienced oil spills and industrial and domestic pollution for years, and the area has been overfished (Cadima et al. 1972, Montesinos 1974). Heavy mercury contamination has been reported in fishes in the Tucacas region (Urich 1981). Pelicans will suffer from oil pollution, not only as individual birds become oiled, but because oil and other pollutants cause decreases in marine productivity, and thus in the food supply of the birds (Schreiber 1980b). Continued overharvesting of fishes, pollution of the marine waters, and destruction of mangroves also may affect the pelican population along the coast of Venezuela.

Summary.—An aerial survey of the coast of Venezuela and its offshore islands (2900 km) conducted during the breeding season of 1983 revealed an estimated population of 17,500 birds in 25 colonies.

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First Bald Eagle nesting record from Sonora, Mexico.—Bald Eagles (*Haliaeetus leucocephalus*) in Mexico are known to breed only on the coast of Baja California (Henny et al., Auk 95:424, 1978; AOU 1983, Check-list of North American Birds. 6th ed., American Ornithologists' Union, Washington, D.C.). In Sonora, Bald Eagles occur regularly in winter in coastal areas and along the Rio Yaqui (Brown and Warren, Wilson Bull. 97:224–226, 1985). Here, we provide the first Bald Eagle nesting record from Sonora and the mainland of Mexico.

On 27 March 1986 we discovered an adult Bald Eagle sitting in a large nest along the Rio Yaqui below the El Novillo dam and reservoir (near 28°45′N, 109°38′W; elevation ca 200 m). The nest was in a 12-m dead mesquite (*Prosopis glandulosa*) 40 m from the river in a riparian woodland that was dominated by mesquite and Goodding willow (*Salix gooddingii*). An adult bird sat in the nest in an incubating posture almost continuously from 11:35 to 18:55 h. To avoid disturbing the adults, we did not check the nest for contents. Two adults were present at the nest the following morning. One adult was on the nest at the start of our observations at 05:58, and, except for leaving for 9 min when the other adult came in to perch beside the nest, it remained there until 10:45 when we left the area. No prey deliveries were observed. The pair also was observed at the nest when it was checked again on 3–4 April. One adult was apparently incubating, and the other adult spent several hours perched on nearby cliffs or trees. Again, no prey deliveries were noted.

No eagles were present at the nest site on 7 May, and the nest was presumed to have failed. One adult eagle was seen 12 km upstream of the nest site on 8 May. There was no evidence (i.e., fecal material on and around the nest) that nestlings had been present. Human activity associated with fence construction along the riverbank within 100 m of the nest may have contributed to abandonment. R. Mesta climbed up into the nest and took minimum and maximum measurements on it (height, 0.6 m; outside diameter, 0.9 to 1.1 m; inside diameter, 0.3 to 0.35 m; inside depth from rim, 10 to 17 cm).

Several large (ca 2 × 5 cm) eggshell fragments were collected from beneath the nest and sent to the Western Foundation of Vertebrate Zoology for identification, storage, and determination of shell thickness; the latter to determine if thinning from DDE or DDT contamination had occurred. The fragments were identified as Bald Eagle eggshells, ranging in thickness (exclusive of associated eggshell membranes) from 0.481 to 0.522 mm ($\bar{x} = 0.502 \pm 0.012$ mm [SD]; N = 15) (L. F. Kiff, pers. comm.). Membrane thickness was estimated at

0.08 mm, for an overall sample thickness of both eggshell and membranes ranging from 0.55 to 0.60 mm. This value compares well with pre-1947 (pre-DDT) Bald Eagle eggshell thicknesses from Florida (0.584 mm) and Texas (0.603 mm) reported by Anderson and Hickey (Proc. Int. Ornithol. Congr. 15:514–540, 1972), and suggests that the Sonora eagle nest did not fail due to eggshell thinning.

A second Bald Eagle nest found 12 km upstream (8 km overland) in March 1986 may have been an alternate nest of the pair we observed. The second nest (height, 1.8 to 2.1 m; outside diameter, 1.2 m; and inside diameter, 0.9 m) was in a 10-m hecho cactus (*Pachycereus pectin-aboriginum*) on a steep, north-facing talus slope overlooking the river. The vegetation at the site was subtropical deciduous woodland dominated by *Jatropha cordata, Bursera fragilis, Lysiloma divaricata,* and kapok (*Cieba acuminata*). On the ground below the nest was a large (ca 20 cm deep) accumulation of sticks, debris, and fecal and prey remains. The relative depth of the nest and the accumulation of debris below it suggested the second nest was older than the active nest downstream. Prey remains below the nest included numerous fish bones and the sternum of an American coot (*Fulica americana*) (T. R. Huels, pers. comm.). Numerous adult Bald Eagle feathers, including two tail feathers, were collected on the ground near this second nest and later deposited with the University of Arizona bird museum. Ospreys (*Pandion haliaetus*) were the only other large, fish-eating raptors that could have been breeding in the vicinity. However, we saw no Osprey nests along the river during our surveys, and Ospreys were not known to nest anywhere within the Rio Yaqui basin (S. M. Russell, pers. comm.).

A 180-km stretch of the lower Rio Yaqui between the El Novillo and Obregon reservoirs was surveyed intensively by boat for Bald Eagle nests between January and April, 1986, resulting in the discovery of these two nests. Several hundred km of perennial riverine habitat in northern Sonora have yet to be surveyed for eagle nests. Clearly, future research is needed to determine the range and abundance of breeding Bald Eagles throughout Sonora. Such information could have substantial implications regarding the recovery of the endangered Bald Eagle population in adjacent Arizona.

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Field observations and comments on the Indigo Macaw (*Anodorhynchus leari*), a highly endangered species from northeastern Brazil.—The Indigo Macaw (*Anodorhynchus leari*) is found locally in Bahia State, Brazil, in the region of the Vaza-Barris river (Sick, Alauda 47: 59–60, 1979). The species was described from captive specimens, and nothing was known about its range and habits until its discovery in the wild by Sick (1979). Here I present information on roosting and feeding behavior of the species and assess the likelihood of its survival. Field work was done from 12 to 30 July 1983.

FIG. 1. Macaw cliff. Note burrows (indicated by white arrows) and droppings on the burrow entrances. Some individuals roost in ablation concavities at left.

Roosting sites and behavior.—The range of the Indigo Macaw is within the "caatinga" region of Brazil, which is dominated by thorny scrub vegetation. Altitude in the region varies from about 380 to 800 m, with daily temperatures varying between 15° and 45°C. Macaws roost in the cliffs or canyons (locally known as "Talhados," or "Serras") that vary in height from 30 to 60 m.

Macaws roost in burrows in the top third of the cliff faces in sedimentary lacunae created by weathering of the sandstone (Fig. 1). Burrow tunnels are fairly narrow, allowing passage of only one individual at a time. As many as 4 birds used a single burrow. Burrows were often within 0.5 m of one another.

Some macaws roosted outside the burrows, clinging to the cliff or shallow shelves. The Indigo Macaw is very shy and quite different from other Macaws, and it has an extensive social organization. Individuals leave their roosting cliffs before dawn for feeding grounds, and return after sunset. Just after sunset, 2 or 3 individuals return to the roost area, flying over the canyon and crying out. They then sit quietly on the tallest tree, cracking the tips of the branches. Trees used by these individuals are easily recognized by the presence of broken branch tips. After about 10 min, these "scouts" begin to call out loudly, and the rest of the flock approaches. The numbers of individuals in the flocks vary. Groups of 22, 33, 19, and 23 were seen on successive days in the same canyon. The birds fly over the canyon screaming, and then land near the scout birds and sit quietly. It is already dark. The birds then begin to scream again as they fly directly to the cliff edge where they sit before quietly entering their nest holes. The "scout" macaws roost in an adjoining canyon. These latter awake before sunrise and fly screaming over the canyon harboring the flock's nest holes. All the macaws then drop out of their holes, and the whole group flies out of sight.

Feeding habitat and behavior.—The Indigo Macaw, like other macaws, feeds largely on hard nuts, which it obtains from palm trees found in the thorn scrub and in pastures cleared

for cattle grazing. Its most important food source is the "licuri" palm (*Syagrus coronata*), which grows on top of the plateau (locally known as "Raso da Catarina") and on crystalline soils in the surrounding lowlands. This palm ranges in height from about 0.7 m to 2.0 m.

I saw flocks of Indigo Macaws feeding on four occasions. The birds feed on palm nuts on palm leaves in small subgroups of 2 or 3 individuals distant 5 to 30 m from one another. They also search the ground (Sick, Int. Counc. Bird Pres. Bull. 1:439–444, 1980) for palm nuts. After they grab a nut with their beak, they fly to a palm tree where they manipulate the nut with their feet, rolling it to remove the pericarpal skin. They then make two transverse cuts before extracting the meat. They open "licuri" nuts (approx. 30 × 20 mm) easily with perfect transverse cuts. There is always a sentinel keeping watch on flocks as they feed. The birds alternate their watching and feeding activities.

Conservation.—The distribution of *A. leari* is located on a contact area of crystalline rocks and sandstone, occupying an extremely small area of only 15,000 km^2 of which 60% has been thoroughly surveyed to date. Only two colonies were localized in the covered area, and the total number of known individuals is 60. On a very optimistic scale, and assuming the remaining 40% of the species' range consists entirely of optimum habitat (which is not very likely), the total population consists of far less than 200 individuals.

Two heavily traveled roads cross this area. The area has been densely populated since the late 1800s, and there are many foot and donkey trails in the area. Hunting is a serious problem. The local human population is very poor, and hunters either eat their catch or sell both live and dead wildlife products in regional markets. The local economy depends on subsistence agriculture and free range cattle and goat farming. The local farmers cut the "caatinga" but leave licuri, which in the dry season provides an important food supply for cattle that eat its racemes and young leaves. Cattle consumption of racemes and unripe fruit may limit the abundance of ripe nuts for macaws. Although macaws prefer mature fruit and cattle prefer green fruit, many farmers believe that macaws compete with cattle for food.

Although many cliffs are seemingly available in the range of *A. leari,* macaws roost in only a few canyons. The reason for this is not known. The present sandstone cliffs that are used as roosting sites are fractured. High thermal variation from day to night produces slides, and a slide occurring at night or during nesting could reduce substantially this rare macaw's population.

Unfortunately, *A. leari* is not protected in any Public Reserve or National Park. The Ecological Station of Raso da Catarina (SEMA—Secretaria Especial do Meio Ambiente) has no resident group of this species. Although *A. leari* sporadically feeds in this "protected" ecological reserve, cattle feed on unripe racemes at the station, and the area furnishes little food.

It is difficult to be optimistic on *A. leari*'s survival as both roosting and feeding areas are privately owned, highly vulnerable, and already subject to considerable human pressure.

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Notes on the Mountain Caracara (*Phalcoboenus megalopterus*) in the Argentine puna.— The Mountain Caracara (*Phalcoboenus megalopterus*) is a conspicuous species in the Argentine puna zone. While not as abundant over large areas of the puna as are other caracaras (*Polyborus* and *Milvago*), in other habitats of Argentina, we found four pairs along the 70 km of road from Cuesta de Auzul Pampa to Abra Pampa, Jujuy Province (3500 m elev.). As is the case with *Polyborus, P. megalopterus* were concentrated near towns where they fed on carrion and refuse. Eighteen individuals were seen from one spot on the outskirts of Abra Pampa as they sat on power poles or fence posts. Three were collected as part of a larger study; 2 at Abra Pampa and 1 at Cuesta de Auzul Pampa. Although they were obtained randomly, all 3 had entire legs or portions of feet missing. Their wounds were healed and appeared to be old. The form of injury was identical to what we have previously seen in raptors that were victims of jaw traps. One adult was missing the right leg about 2 cm below the junction of tibiotarsus and tarsometatarsus, another adult was missing the hallux, and the subadult was missing the entire left foot. Still another adult seen appeared to be lacking an entire foot. Francois Vuilleumier (pers. comm.) has examined 34 specimens of *Phalcoboenus* during the course of his continued interest in caracaras and has noted 3 *Phalcoboenus* with missing toes or feet: One from Chile near the Argentina boundary was missing the foot and had a well-healed leg similar to our finding.

Other genera of caracaras from different habitats have not shown a similar incidence of foot injury. We traveled 6586 km of roads in Northern Argentina and observed more than 400 *Milvago chimango,* 10 *M. chimachima,* and 214 *Polyborus plancus,* and none had conspicuous leg or foot injuries. None of 3 *M. chimango,* 2 *M. chimachima,* and 4 *P. plancus* collected had similar injuries.

Caracaras are unique among Falconidae for building their own stick nests. Brown and

FIG. 1. Left side of the figure shows the cement poles with the nest near the top of the pole. Right side of figure shows a young caracara in the nest.

Amadon (1968) found no instance of caracaras using man-made objects as nest supports, although at least 3 of the 4 species of *Phalcoboenus* do use cliffs in addition to trees and the ground. Five nests of *P. megalopterus* reported by Wolfe (1951) from Chile all were on cliffs with very little nest material (only a few sticks and bits of rubbish). Similarly, Johnson (1965: 265) indicated that all *megalopterus* nests are on cliffs with only "a little dry dung to serve as an apology for a nest." Housse (1938) did not, in fact, find nests, but thought they must nest in trees as some birds ranged down out of the cordilleras into forested country. All of the more than 30 nests of *P. carunculatus* (considered a race of *megalopterus* by Vuilleumier [1970] and Stresemann and Amadon [1979]) studied by DeVries et al. (1983) in Ecuador were on cliffs and seemed to be better constructed than those described above. We could not find references indicating their use of man-made objects for nest placement, but we do not doubt they use them. In the 28 km between Tres Cruces (4200 m elev.) and Abra Pampa, where the road follows a cement high tension power line, we found 2 nests 10 km apart on the cross arms of powerline poles.

The nests were considerably more than a few sticks, bits of dung, and rubbish (both nests were similar in size and construction) (Fig. 1). Sheep or llama wool was also incorporated into the nests. Both nests were substantial, and we suggest that they had been used repeatedly with material added annually. This should, however, also be the case with nests elsewhere on cliffs, and we are unable to explain the differences. The only other species in the puna that could build a nest of similar size are the Red-backed Hawk (*Buteo polyosoma*) and the Puna Hawk (*Buteo poecilochrous*), but their nests are very different in structure from those we found.

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Production of second broods by Northern Bobwhites.—Northern Bobwhites (*Colinus virginianus*) may renest following nest failure if environmental conditions allow (Stoddard 1931), but reports of attempts by unconfined bobwhite females to raise two broods in a single season have not been published. Renesting attempts by captive bobwhites, after hatching initial clutches, have been observed in Missouri (Stanford 1953, 1972) and Texas (Kiel 1976). Francis (1965) described two instances of double-brooding behavior by confined California Quail (*Lophortyx californicus*). Gullion (1956) suggested the occurrence of second broods in wild Gambel's Quail (*L. gambelii*). We describe production of second broods by 2 unconfined female bobwhites.

Reproductive efforts of radio-marked, female bobwhites were monitored from 1 April to 31 October 1984–85 on an area intensively managed for bobwhites in Bullock County, Alabama. Females were fitted with transmitters weighing approximately 4.4 g, in a manner described by Williams et al. (1968). Reproductive behavior was detected near the onset of incubation when telemetry locations indicated relative immobility. Females with broods were located 3 times daily and directly observed at least once weekly to record chick losses and to identify adult-brood association patterns.

Sixteen females that were observed until at least 1 October hatched clutches during 1984–85. Ten of those females hatched clutches after 15 July, but continued associating with their broods and did not incubate again. Broods of 6 other females, whose clutches hatched by 10 July during 1985, disappeared when juveniles ranged from 7 to 35 ($\bar{x}$ = 17) days of age. All first broods that disappeared, except one, were attended exclusively by the female. Immediately after brood disappearance females paired with males, and no association of females with their first broods was subsequently observed.

Four of 6 females, whose first broods disappeared, renested and initiated incubation between 11 August and 3 September 1986. The interval between brood disappearance and renesting, assuming a laying rate of 1.2 days/egg (Klimstra and Roseberry 1975), ranged from 8 to 19 ($\bar{x}$ = 13.5) days. Two females successfully produced second broods, during late September 1985.

It was unclear whether juvenile mortality, brood abandonment (Lehmann 1984), surrogate parenting (Stoddard 1931), or some interaction of the aforementioned was responsible for brood disappearances. Disappearance of entire broods following thermoregulatory independence and after the young were flying suggests that brood abandonment and not mortality may have caused disappearance of some broods. Two unattended broods were observed in close proximity to 2 renesting hens whose first broods disappeared. Lehmann (1984) reported midsummer brood abandonment and the recurrence of adult bobwhites as pairs in southern Texas. Gullion (1956) observed that 60 percent of all Gambel's Quail juveniles were unattended by early July and suggested that brood abandonment facilitated double-brooding.

Our observations raise questions regarding the breeding biology of bobwhites. Must early nesting attempts succeed by mid-July for second brooding to occur as suggested by our data? Does double-brooding contribute significantly to high productivity implied by secondary age ratios during fall? A method for marking bobwhite juveniles is needed to answer these questions.

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Polyandry in a female Northern Mockingbird.—Though the Northern Mockingbird (*Mimus polyglottos*) is thought to be highly monogamous (Laskey 1935), Breitwisch et al. (1986a) and Logan and Rulli (1981) report cases of bigamous males. Here we report the first clearly documented case of a polyandrous female mockingbird.

In spring 1985, two male mockingbirds (M1 and M2), one of which was color banded, occupied adjacent territories on the campus of the University of North Carolina at Greensboro. A single colorbanded female (F1) ranged over both of the territories throughout the 1985 and 1986 breeding seasons. Thirty-two 1-h focal-animal samples were conducted from 14 March 1985 to 3 August 1985. During each observation period the occurrence of six behavioral patterns was recorded. These included conspecific interactions (either between F1 and either male, or between M1 and M2), song, nestbuilding, the feeding of nestlings, F1's perch sites, and incubation.

M1 was observed nestbuilding on 14 March (Fig. 1), but the nest was never completed. On 8 April, M2 was observed nestbuilding, and F1 was seen sitting on the edge of the half-completed nest. The nest, however, was never completed. F1 was observed incubating a nest of 3 eggs in the territory of M1 on 13 April. During the 2 days prior to her laying in the M1 nest, F1 was seen in both males' territories. Both M1 and F1 fed the 3 nestlings that hatched in the M1 nest. During the time she was feeding her nestlings (from 26 April to 3 May), F1 was repeatedly observed in the territories of both males. On two occasions F1 took food from the territory of M2 to feed her nestlings in the territory of M1. The nestlings from the first M1 nest disappeared on 5 May, probably taken by predators. M2 was observed nestbuilding on 10 May, and on 20 May F1 began incubating eggs in the M2 nest. Prior to laying these eggs, F1 was again consistently seen in both males' territories (on

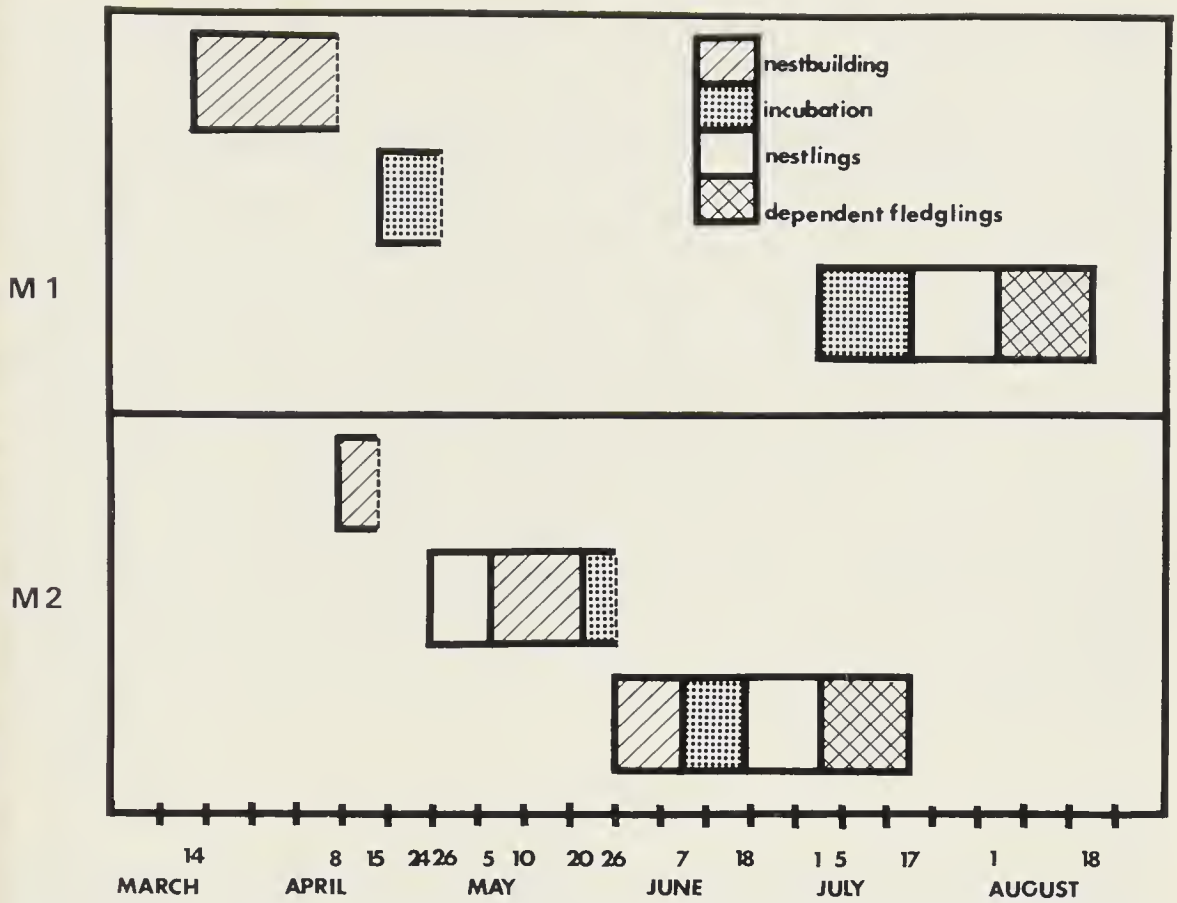

FIG. 1. F1's alternating pattern of activity during the four phases of the breeding cycle: nestbuilding, incubation, nestling, and fledgling, in the territories of two males (M1 and M2) in spring 1985.

15, 17 and 19 May). The first M2 nest was abandoned by 26 May, during a period of heavy rain. M2 immediately began building a new nest. F1 began incubating eggs in the M2 replacement nest on 7 June. Nestlings hatched on 18 June, and both F1 and M2 fed the nestlings. Again, F1 was repeatedly seen in the territories of both males during the nestling phase, and on one occasion she fed her M2 nestlings with food obtained in the territory of M1. Fledging occurred in the first week of July. On 5 July, F1 was found incubating in M1's territory. Though repeatedly sighted in both males' territories while incubating the second M1 nest, during 6 h of observation, F1 was not seen feeding the fledglings from her previous (M2) brood. Eggs from the second M1 nest hatched on 17 July, and both M1 and F1 fed the nestlings. On one occasion F1 fed the M1 nestlings with food obtained in the territory of M2. The 3 M1 nestlings fledged on 1 August; one remained in M1's territory while the other two were found in M2's territory. The mature fledglings from the previous M2 nest had, by this time, left the territory. The young M1 fledglings, now in M2's territory, were fed exclusively by F1. Although M2 was observed perched within 2 m of the fledglings, he was not aggressive toward them, nor did he feed them. The fledgling that remained in M1's territory was fed exclusively by M1.

Although polyandry is thought to be rare in passerines (Jenni 1974, Oring 1982), F1's pattern of alternately nesting with 2 males, the consistent presence of F1 in both males' territories just prior to egg laying, and the lack of aggression by either male directed toward F1 indicate polyandrous mating by this female. The polyandrous strategy of F1 appears to be stable. Although we had not banded the female until 1985, this same pattern had been

observed in the behavior of an unbanded female in the territories of the two adjacent males in both 1983 and 1984. Furthermore, the pattern (Fig. 1) occurred in spring 1986, when F1 again mated alternately with 2 males. We conclude, therefore, that a single female has maintained a stable polyandrous relationship with several males over at least 2, and possibly as many as 4, breeding seasons.

F1 might benefit from polyandrous mating in one of several ways. Although brood overlap (thought to be important in the evolution of polyandry [Erckmann 1983]) is common in Mockingbirds (Logan 1983), the average amount of brood overlap seen in F1 in 1985 and 1986 was within the range of that observed for 8 monogamous females during the same period. The interval between hatching of one brood and incubation of the next (excluding unsuccessful attempts) for F1 was 16 days in 1985 and 23 days in 1986. The comparable interval for 12 broods of 8 monogamous females in the same period ranged from 15 to 44 days (Mann-Whitney U-test $P > 0.10$). F1 lost 2 of 4 (50%) of her nests, whereas 12 monogamous females suffered nest losses of 55% during the spring of 1985. F1 may have gained some advantage over monogamous females from increased predator defense provided by two males (Breitwisch et al. 1986b), though we have no evidence of this possibility. The apparent disadvantage to males of accepting an already mated female rather than mating monogamously may be offset by the skewed sex ratio characteristic of this population in spring 1985 (female : male ratio = 3:4).

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Fish-holding behavior of Marbled Murrelets.—Prey-holding behavior affects the number and size of prey that can be transported to nestlings on each feeding trip and thus the number of trips required to sustain nestling growth (Orians and Pearson 1979). Marbled Murrelets (*Brachyramphus marmoratus*) carry fish in their bills to feed to their nestlings at nests that may be up to 75 km inland from ocean capture sites (Drent and Guiguet 1961; Sealy 1975a; Carter and Sealy 1983, 1986). During studies of the feeding ecology and at-sea distribution of Marbled Murrelets in Barkley Sound, British Columbia, in 1979, 1980, and 1982 (Carter 1984, Sealy and Carter 1984), we saw hundreds of murrelets holding single fish in one of two ways: *crosswise* in the bill with the fish's head held on one side, the tail on the other, at right angles to the bill, with the tomia clamping the sides of the fish (see Drent and Guiguet 1961, Guiguet 1971); and *lengthwise* in the bill with the head held inside the murrelet's mouth, the tail pointed forward and to one side of the bill, with the tomia clamping the dorso-lateral surfaces of the fish (similar to the way murres [*Uria* spp.] often carry fish [see Nørrevang 1958, Gaston and Nettleship 1981]). Pacific sandlance (*Ammodytes hexapterus*) and small Pacific herring (*Clupea harengus*) weighing 2–10 g were held crosswise by murrelets (estimated from observed lengths [see Carter 1984]). Northern anchovies (*Engraulis mordax*) and herring weighing 10–25 g were held lengthwise. Both methods of holding fish were observed while murrelets were on the water or flying, although prey species were identified mainly while birds were on the water.

Marbled Murrelets capture fish underwater but will manipulate fish in their bills after they surface from a dive. Thus, the methods we observed murrelets using to hold and transport fish to nestlings can be different from the methods that they use to capture fish (see Götmark et al. 1986). On 7 June 1979 at 19:50 h, we collected an adult female Marbled Murrelet that was holding an anchovy lengthwise. The salvaged fish (deposited in the University of Manitoba Zoology Museum, Winnipeg) was 110.5 mm long (standard length) and weighed 12.4 g. Its right side was slashed obliquely at midbody below the dorsal fin and there were 2–3 small slashes behind the gill covers. A puncture 5 mm in diameter and 5–10 mm deep was on the side just behind the dorsal fin; it pointed anteriorly. The tomial slashes indicated that earlier the fish had been held crosswise. The puncture apparently was inflicted by spearing during a posterior attack by the murrelet.

Bédard (1969) pointed out that the rigid, cornified tongues of *Brachyramphus* murrelets permit large prey items to be locked firmly against the rows of sharply-pointed palatal denticles. Such modifications of the tongue and denticles are found only in the other narrow-billed alcid genera, *Cepphus* and *Uria*, which also are usually single-prey loaders (Nørrevang 1958, Drent 1965, Birkhead 1976, Asbirk 1979), although occasionally they carry two prey items (Thoreson and Booth 1958, Gaston and Nettleship 1981). Although Marbled Murrelets have been reported carrying 1–6 fish in their bills at once (Savile 1972, Cody 1973), most observations suggest that they usually transport single fish to their nestlings (Simons 1980, Carter 1984). This may answer Bédard's (1976:182) question: "But if one considers as Cody [1973] does that food transport is the most determinant factor bringing about a deepening of the [alcid] bill, how is it then that the Marbled Murrelet which also carries bundles of fish to its inland nestling . . . has one of the shallowest and certainly one of the most unmodified bills of the entire family . . . ?" While the relationship between bill depth and prey transport is unresolved, the Marbled Murrelet is usually a single-prey loader and should not be used as contrary evidence in the above argument.

Different methods of holding fish probably are related to the ratio of prey size : body size, and the properties involved in the expression of force along the mandibles relative to the

bill's shape and size (Bédard 1969, Lederer 1975). Interestingly, *Cepphus, Uria,* and Marbled Murrelets carry similar-sized prey items, yet *Cepphus* usually hold fish crosswise (although rarely lengthwise [Carter, pers. obs.]), *Uria* characteristically hold fish lengthwise, and Marbled Murrelets commonly hold fish both ways. Larger prey may be too awkward if held crosswise (especially when flying) relative to the murrelet's smaller body size (Bédard 1969). The ability of Marbled Murrelets to carry relatively large fish may reduce the number of feeding trips required and partly account for the fast growth rate of young (Simons 1980, Hirsch et al. 1981) compared to other alcids (Sealy 1973). Prey robbery probably has not forced murrelets to hold fish lengthwise because they nest solitarily, do not feed or nest in association with other seabirds, and visit nests mainly at night (Sealy 1975b, Carter 1984, Sealy and Carter 1984). For Common Murres (*Uria aalge*), however, this may be the main selective factor for their manner of holding prey, as they usually nest and feed in dense groups with other seabirds and transport several food loads during daylight (Birkhead 1976).

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Gray Kingbird predation on small fish (*Poecilia* sp.) crossing a sandbar.—The Gray Kingbird (*Tyrannus dominicensis*), a common West Indian flycatcher, normally forages on insects and fruit and has occasionally been reported to prey on lizards (Pinchon, Faune des Antilles Françaises: les Oiseaux, Muséum d'Histoire Naturelle, Fort-de-France, Martinique, 1963; Wunderle, Herpetologica 37:104–108, 1981). Its hunting techniques usually involve catching insects on the wing or picking prey off a substrate while flying. To our knowledge, it has not been reported catching fish. On 3 June 1986, at 07:12 (EST), we witnessed repeated predation by at least two kingbirds on *Poecilia* sp. (*Poeciliidae*) at a partially dried freshwater stream near Holetown, Barbados (West Indies). Several hundred of the fish, a close relative of the aquarium black molly, were attempting to swim upstream from a small pool. Water was <2 cm in most parts of the stream, and sandbars almost totally blocked the stream in several places. At the sandbars, fish moved out of water by a series of short flips for distances of up to 50 cm (a similar mode of locomotion has been documented in the related family *Cyprinidontidae*; Seghers, Verh. Inter. Verein. Limnol. 20:2055–2059, 1979). While on land, at least 11 *Poecilia* were caught and eaten by kingbirds. The birds perched on a branch 10 m from the stream and swooped down over the sandbar, occasionally hovering there for a few seconds. The birds were successful on approximately one third of their attacks. Captured fish were consumed when the birds had returned to their perch. On most occasions, the fish were hammered against the branch before being eaten, a technique Gray Kingbirds are

known to use with insects (Wetmore, Birds of Puerto Rico, United States Department of Agriculture, Washington, 1916). We returned to the site on the next morning but saw neither terrestrial locomotion by *Poecilia* nor fish predation by *T. dominicensis*. On 5 June, heavy rains during the preceding night raised water levels in the stream, and previously discrete pools merged. These observations support Wunderle's (1981) suggestion that island flycatchers may broaden their diet opportunistically by applying their normal hunting techniques to novel prey.

Acknowledgments.—These observations were made out of the Bellairs Research Institute of McGill University, Saint-James, Barbados, and were supported by an NSERC operating grant to LL. We thank D. Kramer for identifying the fish and for various helpful suggestions, as well as J. M. Wunderle for his comments on an earlier version of the manuscript.—Louis Lefebvre and Dominique Spahn, *Dept. Biology, McGill Univ. 1205, avenue Docteur Penfield, Montréal, Québec H3A 1B1, Canada.* *Received 23 Aug. 1986, accepted 10 Nov. 1986.*

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Aerial plunge foraging by a Great Blue Heron.—Wading birds are noted for the plasticity and diversity of their foraging behavior (Kushlan 1978a). Kushlan (1978b) suggests that novel or rare techniques are most likely to be added to the foraging repertoire of wading birds after nesting, when time and energy demands diminish. Individual specialization (Kushlan 1973b) possibly involving learning (Recher and Recher 1972) may increase the efficacy of an uncommon strategy to the point where it becomes an important part of the foraging repertoire of an individual bird. In North America, large wading birds such as the Great Blue Heron (*Ardea herodias*) tend to exhibit less diversity in feeding style than do smaller herons (Kushlan 1976, Willard 1977), and the less common components of their foraging repertoire are not well documented. This report describes the environmental context and behavior of a single Great Blue Heron that repeatedly used plunging (Kushlan 1973a) as a foraging technique.

On 13 October 1977 we observed a Great Blue Heron as it foraged at Tulloch Lake, a large artificial impoundment in the foothills of the central Sierra Nevada, California. The bird made three foraging flights from a large rock outcrop near the water's edge and plunged each time from slow forward flight into water over 10 m in depth. Two of the plunges were successful, and the heron rose from the water with a 10–18 cm bluegill (*Lepomis macrochirus*: Centrarchidae) in its mandibles. On 23 October the same heron (recognized by fishing line tangled around one foot) was observed continuously for 5 h. The fishing line did not appear to preclude normal flying or landing, but its effect on wading ability could not be determined because the bird did not wade. The heron made repeated foraging flights from the same rock outcrop it had used 10 days earlier. The bird obviously oriented toward water disturbances made by surfacing fish. When we threw rocks into the water from our observation point (150 m distant and on the opposite shore from the heron's perch), the heron initiated aerial foraging over the area of the disturbance; it oriented its flight and turned its head toward individual ripples caused by the rocks. Ten of the flights ended in deep water plunges, five of which were successful. After a successful plunge, the heron rose from the water immediately and returned to the rock outcrop where it swallowed its prey (*L. macrochirus*). After unsuccessful plunges, the heron circled over the feeding area, either immediately or after floating on the surface for up to 15 sec. During the two days of observation (5.5 h), the heron made about 20 foraging flights over deep water and plunged 13 times. Seven of the plunges (54%) were successful. During our observations, the heron did not use other foraging techniques and no interactions with other birds were observed.

In large foothill impoundments, bluegill commonly occur in the offshore epilimnion (McGinnis 1984), and during fall they prey heavily on flying insects and other terrestrial arthropods (Goodson 1965), most of which are taken on the surface. We believe the surface activity we saw was normal bluegill feeding behavior.

Our observations were made in October, after the heron nesting season and during the period when intermittent foothill streams, which provide foraging areas during the rest of the year, are dry. At this time shallow water wading sites are scarce. We suggest two environmental factors, a temporary abundance of detectable open water prey and a lack of shallow water wading sites, as proximal stimuli for the plunge foraging spepcialization we observed in this heron. Furthermore, we can not rule out the possibility that the tangle of fishing line around one foot precluded typical foraging.

Acknowledgments.—We thank S. Granholm, T. Highsmith, D. Spector, R. Zink, and the reviewers J. Kushlan and G. Powell for constructive criticism of earlier drafts of this manuscript.

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Allofeeding in American Goldfinches (*Carduelis tristis*).—The passing of food between birds (including individuals of the same sex) outside the breeding season has been termed allofeeding (Smith, Condor 82:291–295, 1980). Previous studies have shown a relationship between allofeeding and dominance. Here, I report allofeeding among American Goldfinches (*Carduelis tristis*) and its relationship to dominance status. Allofeeding has been reported previously in the genus for the Eurasian Siskin (*C. spinus*) (Mundinger, Science 168:480–482, 1971; Senar, Condor 86:213–214, 1984).

I maintained a group of captive American Goldfinches in a 1 × 1.5 × 2 m indoor aviary

at Elkhart Lake, Sheboygan County, Wisconsin, from January through March 1986. The birds were kept in captivity as part of a study on agonistic communication (Popp, in prep.). During January the group consisted of two males (L and R) and two females. The birds were captured, as a group (near a feeding station), in late December 1985. The birds had probably been members of the same flock. All birds were hatching-year individuals at the time of capture. Dominance relationships were determined by observing aggressive encounters that occurred over access to a feeder. A bird was considered dominant to another bird if it won (displaced its opponent) in most of the encounters between them. Dominance relationships were clear-cut between all individuals. Both males were dominant to the females, and L was dominant to R. At the end of January two additional birds (one male, one female) were introduced to the group as part of the main study. At this time there was a change in the dominance hierarchy, with R becoming dominant to L. L and R remained dominant to all other birds. Interactions among the finches at a feeder were videotaped as part of the study of agonistic communication. Additional haphazard observations were made of the goldfinches while they were elsewhere in the enclosure.

Allofeeding was seen 13 times during January (during 20 h of observations). Food was passed in a manner similar to that reported for Eurasian Siskins (Senar 1984). The male giving the food was in an upright posture and made reguritation movements, while the bird receiving the food was in a more crouched posture. In all cases the subordinate bird (R) passed food to the dominant (L). In each case, L solicited from R (by pecking at his beak) before the food was passed. Following the reversal in dominance L was seen soliciting food from R seven times during February (15 h of observation). In all cases R refused to pass food to the now subordinate L, and in four of the cases R directed an agonistic display (head forward display; see Coutlee, Wilson Bull. 79:89–109, 1967) towards L. L stopped soliciting food from R in March.

As both individuals were males, the observed behavior was not courtship feeding. Also, it was not parent-offspring feeding as both individuals were caught as juveniles. That food passing always occurred from the subordinate bird to the dominant bird and that it ceased when dominance was reversed confirms that allofeeding is related to dominance status (cf. Senar 1984).

I thank M. S. Ficken, P. A. Gowaty, G. E. Woolfenden, and L. Bunkfeldt-Popp for their comments on this manuscript.—James W. Popp, *Dept. Biol. Sci., Univ. Wis.–Milwaukee, P.O. Box 413, Milwaukee, Wisconsin 53201.* *Received 30 Sept. 1986, accepted 11 Nov. 1986.*

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Brewer's Blackbird feeding on a Barn Swallow.—At 19:40 on 10 June 1985 we observed an adult male Brewer's Blackbird (*Euphagus cyanocephalus*) feeding on a dead Barn Swallow (*Hirundo rustica*) at the Idaho National Engineering Laboratory, Butte County, Idaho. Our attention was drawn to the blackbird, which was on the ground 70 m off at the edge of a parking lot, because of its conspicuous pecking and plucking movements. We moved to within 50 m and continued observations with 16× binoculars. The blackbird vigorously pecked at the dead bird and ate for ca 5 min, then flew with some flesh in its beak to a nest in low shrubs 150 m from the feeding site. It then flew ca 100 m to a lawn and drank from a small puddle of water. We examined the nest and found 4 approximately 7-day-old blackbird nestlings. Inspection of the partially consumed Barn Swallow revealed that portions of its head, neck, pectoral, and femoral regions had been consumed. Much of the swallow had been plucked. While we were inspecting the Barn Swallow remains, a male Brewer's Blackbird flew briefly into the area and then left.

The cause of the swallow's death is unknown. We assume that the blackbird was opportunistically scavenging. Although invertebrate animal matter comprises a high portion of the blackbird's diet (Bent, U.S. Natl. Mus. Bull. 211, 1938; Horn, Ecology 49:682–694, 1968; Orians and Horn, Ecology 50:930–938, 1969), we know of no other records of Brewer's Blackbirds feeding on a bird.

We are grateful to O. D. Markham and T. D. Reynolds for helpful comments on an earlier draft of this manuscript. These observations were made while conducting Breeding Bird Surveys as part of the Idaho National Engineering Laboratory Radioecology and Ecology Program supported by the Office of Health and Environmental Research, U.S. Department of Energy, and the Idaho Department of Fish and Game.—Leon R. Powers and Mark J. Wheeler, *Dept. Biology, Northwest Nazarene College, Nampa, Idaho 83651.* *Received 6 May 1986, accepted 28 Oct. 1986.*

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ORNITHOLOGICAL LITERATURE

AVIAN BIOLOGY. VOL. VIII. By Donald S. Farner, James R. King, and Kenneth C. Parkes (eds.). Academic Press, New York, New York, 1985: xxiii + 256 pp., 10 black-and-white photos, 8 text figs. $49.50.—Because of the great disparity in subject matter of the two chapters in this volume, each chapter is given a separate review.—(G.A.H.)

Chapter 1.—THE ADAPTIVE SIGNIFICANCE OF COLONIALITY IN BIRDS. By James F. Wittenberger and George L. Hunt, Jr.—Because literature on the evolution of colonial behavior had not yet reached a level of sophistication to warrant inclusion of a chapter on coloniality in "Avian Biology," Wittenberger and Hunt's contribution was not anticipated when the series was originally planned. This situation changed quickly, however, as demonstrated by the proportion (half) of the 500 references used in this paper that were published within the past 10 years. This chapter is a synthesis of the rapidly growing literature on the adaptive significance of coloniality, and the authors begin by outlining their objectives: (1) to evaluate existing hypotheses for explaining the evolution of colonial behavior, (2) to identify the evidence still needed to test them, and (3) to present new hypotheses and perspectives where current thinking seems inadequate. Their ultimate goal is to achieve a more integrated body of knowledge that will enhance our current understanding of avian coloniality and help focus future research on important unanswered questions.

A section follows the Introduction in which the authors define their use of the term "colony" and review the occurrence of coloniality among birds. They define a colony as "a place where a number of individuals or pairs nest or regularly roost at a more or less centralized location from which they recurrently depart in search of food." Because the term colony typically is used to refer to a group of individuals rather than to the location where they congregate (e.g., see Kushlan's recent commentary on terminology, Colonial Waterbirds 9:119–120, 1986) this definition surely will make some readers uncomfortable; others will disagree with the inclusion of nonbreeding assemblages of birds in this review. The authors obviously anticipated some of these criticisms and carefully justified their definition as one that allows a parallel discussion of breeding and roosting systems which they deemed desirable because in some cases theories developed for one system are applicable to both.

Some of the more stimulating ideas found in the entire chapter are in the next section titled "Toward a Better Theoretical Perspective." Here the authors point out that a common approach to studying the evolution of colonial behavior is to catalog the costs and benefits experienced by individuals that live in groups and to identify the benefit with the greatest positive effect as the most likely reason why coloniality evolved (or conversely, the cost with the greatest negative effect is used to explain why a given option has not been adopted). Wittenberger and Hunt emphasize that this approach has major problems: (1) it implies a single selective pressure has been responsible for the evolution of a behavioral trait, and (2) it fails to consider that many variables may enter the argument as both a cost and a benefit (e.g., colonial behavior may attract predators [cost]; colonial behavior may enhance predator deterrence [benefit]). The authors propose that a more comprehensive approach is to consider the net effect of coloniality. To demonstrate the usefulness of this direction they use the next five sections of the chapter to examine the net effect that coloniality has on food intake ("Energetic Effects"), predation pressure ("Predation Effects"), conspecific interference ("Egg Destruction and Chick Killing"), mate acquisition ("Extrapair Copulations"), and miscellaneous factors ("Other Considerations"). The authors evaluate the evidence available to support each factor hypothesized to favor colonial behavior and present the reader with a

clear picture of questions yet to be answered as well as good suggestions for future lines of research. I did have problems with the section on "Egg Destruction and Chick Killing" in which the authors state that increased egg and chick loss due to the presence or activities of conspecifics represents a potentially severe cost of coloniality. The nature of their discussion implies that they accept that loss of chicks and eggs to conspecifics is a widespread and normal event. Numerous studies have documented that the presence of investigators in colonies causes egg and chick loss to conspecifics. Shugart and his coworkers (Wilson Bull. 93:565–569, 1981) recently documented that chick mortality in Herring Gull (*Larus argentatus*) and Caspian Tern (*Sterna caspia*) colonies could be decreased significantly by minimizing investigator disturbance using a system of tunnels to gain access to blinds. Based on their results, I will not be convinced that studies of chick deaths caused by neighboring conspecifics tell us anything about the evolutionary history of a population unless investigators have taken precautions similar to those outlined by these authors.

In the last two sections, Wittenberger and Hunt evaluate the net effect of factors influencing coloniality and summarize their synthesis with the following conclusions: (1) the adaptive significance of avian coloniality is not yet understood, and (2) no single hypothesis is likely to provide a general explanation of avian coloniality. The authors recommend that investigators focus on testing the more important predictions that arise from the variety of hypotheses that have been proposed to explain why coloniality evolves; in addition, they suggest another important task is to delineate different forms of coloniality that are associated with a distinctive set of selective factors.

Wittenberger and Hunt have produced an important synthesis that students of social behavior will read to obtain a current perspective of this exciting topic; some will continue to use it as a springboard to new research directions, as this chapter is infused with enough new ideas to keep many investigators busy for decades.—FRANCESCA J. CUTHBERT.

Chapter 2.—THE FOSSIL RECORD OF BIRDS. By Storrs L. Olson.—Olson's contribution covers a much wider field than the title suggests. That interest in paleornithology is increasing is evidenced by the fact that over 60% of the 500 references cited by Olson were published within the last 15 years, approximately the period since the publication of Brodkorb's 1971 "Catalog of Fossil Birds" that brought all nonpasserine fossil records up to date. At least 100 have appeared within the last five years. For the paleontologist, therefore, the chapter provides a valuable source of up-to-date information, including unpublished studies now in progress.

Of equal importance to the recording of fossil species, genera, etc., is the interpretation of what this knowledge reveals with regard to relationships and distribution of modern birds. It is in this area that all ornithologists will profit from careful perusal of the analyses provided.

In his introduction Olson states that the Chapter does not pretend to treat the entire fossil record of birds. He has, instead, concentrated on the Mesozoic and Tertiary history of the group in an attempt to relate what he believes "paleontology currently tells us about the first appearance and evolution of the major taxa."

The analysis of Mesozoic birds includes recently published fossil records from the Cretaceous of Mongolia, Russia, and Baja California. The most notable of these, from the Lower Cretaceous of Mongolia, was *Ambiortus*, a volant bird that exhibits similarities to a recently reported, but unnamed, paleognathous carinate from the Eocene of North America. Although, for the most part, the Mesozoic birds are maintained in extinct orders, Olson indicates that the Charadriiformes and possibly the Procellariiformes are also represented.

Twelve pages are devoted to the paleognathous birds and their possible origin. Morphological studies of living birds, as well as the fossil record, are included. Ornithologists who are involved in studies of this group of birds will find much of significance in Olson's treatment of the various theories of their origin.

Olson notes that the present classification of birds "in no way reflects the probable evolutionary history of the class." The fossil record of extant orders is, therefore, presented in what he terms a "working arrangement" based on the assumption that birds originated on land and that highly specialized water birds (such as loons and penguins) are the most derived. The latter half of the Chapter is, therefore, arranged under the headings of "Basal" Land Bird Assemblage, "Higher" Land Bird Assemblage, and Waterbird Assemblage. Should the reader find this arrangement difficult to follow, the carefully prepared index (which, however, includes subject matter for Chapter 1 as well as Chapter 2) provides a ready means of locating a desired taxon.

The "Basal" Land Bird Assemblage includes the Galliformes, Cuculiformes, Falconiformes, Columbiformes, and Psittaciformes. But, as Olson notes that the ordinal limits in this group need redefinition, many of the birds discussed are at the family level.

The remaining land birds are treated at length under the "Higher" assemblage, with revision particularly in the Coraciformes and Piciformes, both of which are considered to be polyphyletic.

Several innovations are offered in the Waterbird Assemblage. Notable among these, the probable evolution of ostriches (Struthionidae) from three Eocene and Oligocene crane-like birds, is discussed under the Gruiformes. Olson adds that these early families (Geranoididae, Eogruidae, Ergilornithidae) "will perhaps later be combined under the Struthionidae much as *Hyracotherium* ("*Eohippus*") and later horses are all placed in the Equidae." The "New World Vultures" (Vulturidae = Cathartidae) and the extinct Teratornithidae are included in the Ciconiiformes. Regarding the Vulturidae, the fossil record suggests that "New World" is a misnomer for this group. The ibises (Plataleidae) are considered "mosaics of gruiform and charadriiform characters." The flamingos (Phoenicopteridae) are placed in the Charadriiformes. The excellent record of the charadriiform genus *Presbyornis* is cited as indicating that the Order Anseriformes likely evolved from a primitive charadriiform ancestor, a conclusion of especial interest to me in view of my study of the South American Eocene *Telmabates* (later synonymized with *Presbyornis*). I found in *Telmabates* a synthesis of flamingoid (now charadriiform) and anseriform characters so notably evidenced that I often, jokingly, referred to the bird as a "flamoose." Although Olson agrees with Storer that loons, grebes, and hesperornithiforms did not share a common diving ancestor, he questions Storer's suggestion of a charadriiform ancestry for loons, and proposes a closer relationship to the Procellariiformes and Sphenisciformes—adding, however, that "the evidence is as yet quite tentative."

The message Olson conveys throughout this Chapter is that the fossil record of birds is very much alive. Not only are there continuing studies from sites in North America and Europe, but new discoveries are coming from Mongolia, South America, Australia, and China. Many of these suggest distributional, as well as anatomical, changes within the avian groups recognized today. We may not agree with all the conclusions Olson offers, but the Chapter is a challenge to preconceived ideas.—HILDEGARDE HOWARD.

PROCEEDINGS OF THE FIFTH PAN AFRICAN ORNITHOLOGICAL CONGRESS. Edited by J. Ledger. South African Ornithological Society, Johannesburg, 1984:885 pp. $45.00 (paper).—The Pan African Congress is unique, there being no other continental ornithological congress. The present Congress met at Lilongwe, Malawi, in 1980. Its proceedings were published December 1984. (A Sixth Congress convened in 1985.)

The 57 papers of the Congress are grouped under seven sections: "Systematics," 4 papers; "Population Studies," 6; "Ecology," 18; "Miscellaneous," 7; "Conservation," 8; "Behavior," 4; and "Breeding Biology," 10. Numbers of papers within these sections may be more or

less indicative of current (1980) emphases of investigation regarding the African avifauna. Review of the papers probably affords a reasonable sample of ongoing ornithological research in that continent.

"Systematics" is introduced by a 13-page edited version of a manuscript by the late Leslie Brown: "Systematic Problems in African Falconiformes." T. Farkas' "Taxonomic Features Common to Mimidae, *Erythropygia* and Some Other Genera" concludes that African genera surveyed and the New World Mimidae probably have descendancy from ancestors of the Timaliinae. This reviewer became uncomfortable at ruling out convergence for many of the characters selected to suggest homology (e.g., rounded wings, colored irides, etc.). I found "*Corythornis* Systematics and Character Release in the Gulf of Guinea Islands" (C. H. Fry and R. de Naurois) and "Secondary Contacts in Central Africa" (A. Prigogine) substantial papers.

"Population Studies" range from treatment of a single species, "The Brown-throated Golden Weaver (*Ploceus xanthopterus*) from Moçambique and Malawi" (D. N. Hanmer) to "Population Dynamics of Birds in *Brachystegia* Woodland" (C. J. Vernon). In "Changes in the Avian Population of the Kalahari National Park," R. Liversidge grouped 63,427 bird sightings by feeding habits and plotted these data against rainfall. The conclusion: in semiarid areas "nomadism and rapid reproduction enable birds to capitalize on the super abundance of food resources which occurs after good rains." In "Studies of Birds in a Semi-arid Region of Kenya," D. E. Pomeroy and C. Muringo report that highest avian densities correlated with rainfall of 400–600 mm/yr (highest mammalian densities at >1000 mm/yr). Again bird mobility is emphasized, this enabling effective exploitation of food resources subsequent to unpredictable rainfall. D. B. Hanmer's "Life Expectancy and Productivity Estimates for Three Species of Bulbul from Southern Malawi" provides useful data for comparison with other passerine species. Considering the tempo of change of African landscapes, one wishes that population studies could be increased manyfold.

"Ecology" offers one third of the papers. Many emphasize G. J. Morel's comment ("Congress Review," pp. 27–30) that the Congress "provides more facts than theories." Two papers discuss waterfowl distribution, but a blank page (p. 403) eliminates figures. Raptor diversity and density in Zimbabwe are discussed and habitat preferences of 16 species of Zimbabwe rails are described. A blank page (p. 390) diminishes appreciation of a paper regarding the ecology of South African kingfishers. Two papers on vultures deal with: scavenging in South Africa (P. R. K. Richardson) and a comparison of food supplies of African and South American vultures (D. C. Houston). The statement (p. 251) that "most of the New World vultures are found in areas of dense rain forests" needs qualification. M. Louette's "Apparent Range Gaps in African Forest Birds" is interesting. J. M. Winterbottom's "Islands and 'Islands' in Bird Distribution" re-emphasizes that avifaunas of ecologically isolated areas within continents can exhibit characteristics of those of oceanic islands.

Four of the "Ecology" papers describe responses of native birds to "disturbed" habitats. Rameron Pigeons (*Columba arquatrix*), frugivores important in seed dispersal of indigenous trees, have "shifted their niche" to Natal's exotic flora (T. B. Oatley). Also in Natal, Thick-billed Weavers (*Amblyospiza albifrons*) adapt to agricultural areas as these replace forest habitats (H. T. Laycock). Pest statuses of some granivorous birds of Kenya are discussed by N. N. Gichuki. Changes in population and division of resources of four birds of the Benguela upwelling system are correlated with commercial fisheries' activities (J. Cooper). Numbers of Jackass Penguins (*Spheniscus demersus*) have decreased fourfold in 24 years.

A. Guillet's "Ecological and Ethological Aspects of the Nest of the Shoebill" is welcome. G. C. Backhurst and D. J. Pearson extrapolated numbers of migrants at lights to probable numbers and timing of Palaearctic migrations over southeast Kenya. F. Dowsett-Lemaire and R. J. Dowsett evaluated forest size regarding montane bird populations of the Nyika

Plateau. Groupings of small forests rather than a few large ones were found to achieve higher densities of many species. To be noted is D. N. Johnson's study of two "similar" flycatchers (genera *Tchitrea* and *Dyaphorophyia*) of the Nigerian rain forest. Where territories of these overlapped, competition was not discernible: it is suggested that given ample food and commodities, "high niche" overlaps are ecologically feasible.

In a "Miscellaneous" paper E. C. Collias evaluated 1000+ eggs produced by 34 female Village Weavers (*Ploceus cucullatus*) during their lifetimes. Sizes, shapes, color, and aspects of spotting were statistically consistent for each bird. He suggests that a female can discriminate between her eggs and variably similar eggs of a brood parasite, the Didric Cuckoo (*Chrysococcyx caprius*). A. J. F. K. Craig postulates that multiple nests built by monogamous male Spectacled Weavers (*P. ocularis*) suggest a "mechanism" whereby the widespread polygyny in weavers could have originated. Techniques for monitoring weights of adult and nestling bee eaters are described by C. H. Fry et al. Among information possible from chemical profiles of feathers is knowledge of where, geographically, the feathers were "grown" (J. P. Kelsall). Finally, there is an interesting contribution to natural history of the Madagascar ground rollers (D. A. Turner).

"Behavior's" four papers feature analysis of almost 1800 h of Black Eagle (*Aquila verreauxii*) activities (V. Gargett), nonbreeding behavior of African Black Oystercatchers (*Haematopus moquini*) at offshore islands (P. A. R. Hockey), group sizes of Cape Turtle Doves (*Streptopelia capicola*) at desert waterholes (W. R. Siegfried), and duetting in some ground barbets (L. L. Short and J. F. M. Horne).

"Breeding Biology" offers the second largest number of papers, data of some affording thresholds for theorizing. Blackshouldered Kites (*Elanus caeruleus*), for successful breeding, depend upon seldomly predictable maximum rodent populations (J. Mendelsohn). As they breed whenever suitable feeding conditions arise, it is theorized that some feature of the prey before a peak of abundance triggers reproduction; four are suggested. White-fronted Sandplovers (*Charadrius marginatus*) of South Africa are paired and territorial throughout the year, adaptations, it is believed by A. A. and T. M. Crowe, for opportunistic breeding (e.g., "close pairing allowing quick response to suitable conditions"). The late L. H. and C. H. Brown question food supply as the "main determinant" of breeding in African birds. E. K. Urban sets the normal annual figure of breeding pairs of White Pelicans (*Pelecanus onocrotalus*) in Africa between 10,000 and 40,000. N. E. Collias reports on behavior and reproduction in the heretofore little known Grey-capped Social Weaver (*Pseudonigrita arnaudi*). From Mali, R. T. and M. P. Wilson contribute to knowledge of Hammerkop (*Scopus umbretta*) breeding biology. There is discussion of sibling aggression and chick starvation of African Fish Eagles (*Haliaeetus vocifer*) in Uganda (S. J. A. Sumba). The Didric Cuckoo, from frequency of parasitism and degree of likeness of its eggs to those of its hosts, is shown to have host-specific gentes (J. F. R. Colebrook-Robjent). C. J. Vernon presents evidence that the Thickbilled Cuckoo (*Pachycoccyx audeberti*) is promiscuous. The effect of position in hatching sequence on the growth of Jackass Penguin chicks is documented by A. J. Williams and J. Cooper.

"Conservation" opens some "windows" into the changing African landscape. In "An Assessment of Rare, Vulnerable and Endangered South African Breeding Birds," R. K. Brooke applied the Landry Scale to the 167 species of the "South African Red Data Book." Six were deemed in need of more protection and active management, 70 in need of ongoing monitoring. Attesting all too eloquently to civilization's effects is the Yellow-billed Oxpecker (*Buphagus africanus*), which no longer breeds in South Africa; the game with which the species was symbiotic is largely gone and thus, too, the ticks the birds feed upon. Potential symbionts, cattle, are dipped in arsenic to control ticks. A. F. Boshoff and C. J. Vernon sent

questionnaires to *all* farmers of South Africa's Cape Province; 14,800 (48%) replied! Because conservation of raptors apparently depends largely upon the farming community, increased conservation education is urged. Cape Vultures (*Gyps coprotheres*) now number but 50 breeding pairs in the Province. On the other hand, Red-breasted Sparrow Hawks (*Accipiter rufiventris*), colonists of homestead tree-claims, have increased, and so have African Fish Eagles in response to increasing numbers of water impoundments. P. L. Britton et al. ("East African Endangered Species") found that 9 of the 10 endangered species are forest birds and pronounced that the Uluguru Bush-Shrike (*Malaconotus alius*) may have become "Africa's first avian extinction."

Seven of the eight "Conservation" papers are by delegates from South Africa. R. K. Brooke writes (p. 569): "South Africa's public consciousness of its need to conserve its avifauna is both quite developed and quite well oriented to those species which need it." Laudable indeed. But only two areas outside South Africa are subjects of "Conservation" papers. There are nearly 50 "countries" in Africa—what of the rest of them?

Inspection of the list of Congress delegates elicits a somber note. I count only 11 African "countries" represented—about 20%. There are, of course, other organs for reporting research in Africa. Whether or not the Proceedings affords a "barometer" regarding ornithological activity in the continent is uncertain. Attending this Congress were 118 delegates. There were 250 at the Fourth Congress and 217 at the Third. A reviewer may not have "license" to stray from the role of textual criticism; however, in review of the Congress, Morel (p. 29) wrote that outside of South Africa the resident ornithologist is "on the decline" and "endangered." Education and incentive from governments, he believes, are necessary to remedy this situation. We can but try to be optimistic that, as Morel hopes, we can "absolutely make the governments understand that ornithology, especially in Africa, is necessary." A heritage, both unique and magnificent, is slipping rapidly away from us. We need to learn all we can of it now—that we can wisely conserve and document what we still have. If we do not accelerate research, we will surely, as Moreau (Bird Faunas of Africa and its Islands 1966:vii) put it, be reduced to "scrabble about in the ruins of . . . a flora and fauna" in reconstructing what was there.

The Fifth Proceedings contains a wealth of ornithology. Its editor is to be commended on a presumably difficult task well done. The volume should be available to all serious students of vertebrate biology. Much will be gleaned from it. Additionally, many will, as did I, find the papers interesting and pleasant reading.—Oscar T. Owre.

Life of the Woodpecker. By Alexander F. Skutch, illus. by Dana Gardner. Ibis Publ. Co., Santa Monica, California, 1985:136 pp., 67 color plates. $49.95.—Alexander Skutch has long been one of my favorite authors and ornithologists; perhaps it has been his sense of intimacy with individual species, perhaps the lure of the Central American habitats he has often written about. With my own interest in woodpeckers, it was with great anticipation that I began reading "Life of the Woodpecker."

"Life of the Woodpecker" is a coffee-table sized book (24 × 31 cm) that is lavishly illustrated with color plates. It seems to be intended for the serious amateur, but it is a fascinating book—perhaps because woodpeckers have such amazing structural and behavioral adaptations—that holds something for anyone with at least a casual interest in nature. Yet Skutch's intimacy with rarely studied Central American woodpeckers provides meat for even the most advanced woodpecker "specialist."

The book begins with a discussion of the position of woodpeckers among the birds of the world, then details the woodpecker niche: how they get their food, where they make their

homes, and what they do within their environment. Other chapters deal with (1) vocalizations, drumming, and displays; (2) nesting; (3) fledged young; (4) social life; (5) usurpers, parasites, and predators; and (6) woodpeckers and man.

Skutch relies greatly on his own experiences in each chapter, but also draws freely from the technical literature. His coverage of the literature, while far from comprehensive, is good. A Literature Cited section with entries arranged by chapter includes approximately 107 references to the technical literature and will be very useful to budding "picophiles." Admirably, Skutch makes extensive use of the German literature.

In spite of enjoying the book, I was at times very frustrated with it. There are more than an average number of typographical errors, and many sentences are shy of needed commas.

Although there is a glowing introduction by S. Dillon Ripley, there is no acknowledgments section, and it appears that no woodpecker specialist reviewed the manuscript for accuracy. As a result, there are a few inaccuracies. For example, Skutch tells us (p. 11) that woodpeckers have a "white tongue." I have examined the tongues of living adults and nestlings of seven species of woodpeckers in eastern North America and the tongue of an adult Black-cheeked Woodpecker (*Melanerpes pucherani*) from Costa Rica. The nestlings do have a white tip on their pink tongue, but all of the adults have had a slate or darker gray tip on a pink tongue. The white tip of the tongue is the central of five spots of white on the nestlings of many species of woodpeckers (the other four are egg teeth on upper and lower mandibles and oral flanges). These white areas seem to form a "target" that facilitates feeding of the young by the adults in the dark cavity.

An error that is more obvious is on p. 37, where Skutch informs us that "Only one other North American bird besides the Northern Flicker (the Mourning Dove [*Zenaida macroura*]) nests in all of the 49 mainland United States." Indeed, there are several species that have such a range, including the Hairy Woodpecker (*Picoides villosus*) and Downy Woodpecker (*P. pubescens*).

I question the suggestion (p. 11) that the barbed tongue of woodpeckers functions in capture of soft-bodied insects by piercing them, implying that the barbs then keep the skewered prey from slipping off the tongue on the way out of the tree. Logic suggests that isn't the case. If it were, how would the woodpecker then remove the prey from his tongue to swallow them? My observations of captive Red-bellied (*M. carolinus*) and Red-cockaded (*P. borealis*) woodpeckers indicate that the tongue extends into a tunnel or crevice beyond a prey item and that in withdrawing the tongue, the saliva coated barbs drag along the prey.

The color plates are generally fine illustrations that add to the appeal and usefulness of the book. Tree surfaces and the minimal backgrounds of most are generally appropriate, and compositions are pleasing. Most birds, however, are flat and a few seem misproportioned (e.g., the Downy Woodpecker, p. 60, has a large head-to-body ratio). Many have exceptionally small eyes (e.g., the Hairy Woodpecker, p. 56). I found the Ladder-backed Woodpecker (*P. scalaris,* p. 116) to be one of the more pleasing illustrations.

My favorite chapter is the last one, in which Skutch discusses similarities between woodpeckers and men, and the problems each creates for the other. He concludes by sounding an alarm that we have heard all too frequently in recent years: "Already many beautiful species, of whose habits we know next to nothing, are threatened by the appalling destruction of tropical forests." We are indebted to Skutch, for he is one who has made us aware of these species, the beauty, and the threats.—JEROME A. JACKSON.

AN ANALYSIS OF PHYSICAL, PHYSIOLOGICAL, AND OPTICAL ASPECTS OF AVIAN COLORATION WITH EMPHASIS ON WOOD-WARBLERS. By Edward H. Burtt, Jr. Ornithol. Monog. 38, American Ornithologists' Union, Washington, D.C., 1986:126 pp. $15.00.—The coloration of

birds is among their most obvious yet least understood features. Why are birds colored as they are? The question has elicited many conjectures and observational explanations but hitherto little rigorous study. This monograph makes a bold advance toward some solid answers and shows that the problem is amenable to further testing.

Burtt examines a series of hypotheses that may account for the evolution of a particular color or color pattern in birds. Resistance to abrasion, energy balance, minimizing reflection that interferes with vision, creation of optical signals during routine or display behavior, and contrast with the coloration of the habitat are investigated. These ideas are tested with wood-warblers (Parulinae), an appropriate choice as the author explains.

Prompted by long-standing observations, Burtt conducted experiments that confirmed that black parts of feathers are more abrasion-resistant than white parts. His findings suggest that durability may be a selective factor in the evolution of melanic colors and patterns. He notes that the dark dorsal, pale ventral pattern that is common among wood-warblers may be due to countershading for concealment as well as abrasion-resistance of the back. These theories are not mutually exclusive and cannot now be separated.

Hypothesizing that the color of the legs and the mandibles might be a factor in behavioral energetics, Burtt examines the energy flow for these structures. He develops an equation to test this idea and applies it to large sets of field observations on leg and bill postures. Leg color is found to affect energy absorption but yet be unrelated to potential convective heat loss. Further analysis confirms that dark-legged warblers "are able to arrive earlier and remain later on their northern breeding grounds" than pale-legged species. The latter spend the winter in warmer regions than the former. Mandible color, by contrast, appears to be unimportant for energy flow in these birds and probably evolved under other selective pressures.

Analysis of colors and behavioral observations indicates that in warblers, "color of the upper mandible is an adaptation to minimize reflection that interferes with vision." The facial markings do not seem related to reflectance but may serve other visual functions.

Conspicuous color patterns, exemplified by wingbars and tailspots, are found, not surprisingly, to be associated with movements that display them. The complex evolutionary relationship between the patterns and the behavior is beyond the scope of this study.

Lastly, Burtt investigates whether the colors of warblers may have evolved so as to contrast with their background habitat. After an elaborate explanation of theory and methodology, he quantifies the "color-space" of his birds (i.e., differences in the light in different kinds of forest and at different times of spring). Subsequent analysis of behavioral observations on American Redstarts (*Setophaga ruticilla*) and Yellow Warblers (*Dendroica petechia*) supports his hypothesis but does not rule out other possible selective forces. The argument is hedged with assumptions and limitations, and its conclusion is very modest in proportion to the long preamble. Nevertheless, the notion of color space appears to deserve further exploration, especially with woodland birds.

This study adds some new ideas to the many that have already been advanced to account for the coloration of animals. More importantly, it tests some existing ideas and demonstrates the value of a quantitative, predictive approach to the subject. Burtt offers explicit hypotheses and shapes his experiments or fieldwork to give clear answers. These results yield new predictions, which are themselves tested. The author appears to understand well energy balance and color vision (beyond this reviewer's competence to judge). At the same time, he recognizes the assumptions and limitations of his "evolutiono-engineering" approach—chiefly that it ignores evolutionary history.

The monograph has been carefully written and edited. Although it retains a measure of typical dissertation style, this has been leavened by apt quotations at the chapter headings, some chosen from Will Cuppy, Kenneth Grahame, and A. A. Milne. It is furnished with illustrations, references, and appendices of supplementary information.

Burtt's approach and findings significantly advance our understanding of the possible selective pressures in the evolution of colors and color patterns in warblers. One hopes that his lead will be followed with other groups and in other habitats.—PETER STETTENHEIM.

BIRDS IN SCOTLAND. By Valerie M. Thom. T. and A. D. Poyser, Carlton, England, 1986: 392 pp., 151 drawings, 173 distribution maps, 33 photos, many diagrams. £24.00 (distributed in the U.S. by Buteo Books, Vermillion, South Dakota, $47.50).—Scotland is a small country, covering 7,720,000 ha (29,806 mi^2), falling in size between the 40th (West Virginia) and 41st (South Carolina) of the states of the U.S. However, it has almost 4000 km of mainland coast, plus 126 inhabited and 664 uninhabited islands, which add another 6300 km of coastline. It is therefore hardly surprising that slightly more than 50% of the space devoted to species accounts in this fine book deals with water birds, whereas these groups occupy less than 38% of the species accounts in Sprunt and Chamberlain's "South Carolina Bird Life."

For many of us inlanders, the 1966 cruise of the "Devonia" around the periphery of Scotland was our first, and highly memorable, exposure to northern seabird colonies. Although gross and relative numbers of seabird species have varied over the years, one feels that their habitats have persisted with little change since before mankind reached the British Isles. The Scottish mainland, however, bears little resemblance to its original state. At present, according to Valerie Thom, 63% of the area of Scotland is devoted to "rough grazing and ungrazed uplands," 23% to agriculture (including pasture), and only 11% to productive forest (the missing 3% presumably being urbanized). The original Scottish forest was dominated by Scots pine and birch in the north and oak and ash in the south. Very little native woodland can now be found in Scotland, and "even the planted broadleaf woodlands characteristic of the big lowland estates are dwindling." Yet the total area of woodland increased by about 75% between 1947–49 and 1979–80. This increase has been brought about by massive planting ("afforestation" in Britain) of conifers—not, unfortunately, the native Scots pine, but chiefly with Sitka spruce and Lodgepole pine from North America. Such plantings are even encroaching on large areas of the classical heather moorlands, the preferred habitat of such species as the Merlin (*Falco columbarius*), Greater Golden-Plover (*Pluvialis apricaria*), and Red Grouse (*Lagopus lagopus*).

All of these dramatic changes in ecology help to explain why a new major work on the birds of Scotland was needed only some 30 years after the publication of the (then) definitive two-volume work "The Birds of Scotland" (1953) by E. V. Baxter and L. J. Rintoul. Much of the emphasis of Thom's book is thus, understandably, on changes in status, especially on details of distribution and population sizes. The distribution maps for individual species do not attempt to show historical changes, but do differentiate, by variations in hatching, areas of widespread versus scarce or sporadic distribution. As a purely local avifauna, "Birds in Scotland" omits any reference to extralimital distribution, nor does it attempt to emulate most of the American state bird books by including field marks or expensive color plates. The text is nevertheless enlivened by small, attractive line and wash drawings of birds, created by a team of 13 people under the direction of Donald Watson, dean of Scottish bird artists (who also contributed a handsome color painting of a family of Arctic Loons [*Gavia arctica*], reproduced, unfortunately, only on the dust jacket).

I found the 11 introductory chapters especially interesting and surprisingly thorough considering their brevity (averaging 4.3 double-column pages). They include "Scotland—its avifauna and geography," followed by 6 chapters devoted to particular habitats. Then come "Developments in bird study," "Protection and conservation—progress and prob-

lems," and "Recent changes in status and distribution," all emphasizing changes since the publication of Baxter and Rintoul's book. The last introductory chapter gives the "Background to the species accounts."

British reviewers, with their specialized knowledge, have been able to spot a few errors and omissions (see Furness, Bird Study 33:144, 1986; and Boyd, Scottish Birds 14:44, 1986), but have been as enthusiastic about the book overall as is the present reviewer.

In view of my decidedly favorable impression of "Birds in Scotland," it is tempting to say to authors and organizations contemplating the preparation of regional avifaunas in North America, "Go thou and do likewise." One must wonder, however, whether there is, in any comparable area of this continent, a group as devotedly enthusiastic, knowledgeable, and downright numerous as the Scottish Ornithologists' Club (which sponsored this book), plus supporting national organizations comparable to the three that supplied major assistance to the project: the British Trust for Ornithology, the Wildfowl Trust, and the Royal Society for the Protection of Birds. Although there is no question about the tremendous accomplishment of Valerie Thom, that this was truly a cooperative project is indicated by a reading of the two full pages devoted to acknowledgments.

Because it is, after all, highly local in its coverage, I can recommend "Birds in Scotland" chiefly to two audiences: those especially interested in British birds and those who wish to study the book as an exemplary model for a regional avifauna.—KENNETH C. PARKES.

MONTEREY BIRDS. By Don Roberson. Monterey Peninsula Audubon Society, Carmel, California, 1985:266 pp., 64 color plates, 24 black-and-white plates, individual breeding range maps, temporal bar graphs. $14.95.—Monterey County, California, including the offshore waters up to 200 miles from land, comprises the geographic scope of this latest work by Roberson. This is the first study devoted exclusively to the status and distribution of the 427 species of birds found in the fourth most well-endowed county in California. Although various state and regional works form the backbone of the present work, Roberson draws upon unpublished field notes and articles from numerous journals. The book is an important contribution, despite some flaws. I recommend it to a limited audience.

Twenty-eight introductory pages precede the species accounts. An all too brief description of habitat features and general bird distributions includes a confusing discussion of the unique pelagic conditions that account for the occurrence of many uncommon species and a few of the rarest North American species within and beyond Monterey Bay. The text describes the locations of the Davidson Seamount, the Monterey Bay submarine canyon, and the Santa Lucia Escarpment in feet and miles. The accompanying map (using fathoms and statute miles) labels none of these features. The pelagic extensions of the northern and southern boundaries of Monterey County are not explained and encroach upon an area seemingly within San Luis Obispo County to the south. Roberson acknowledges that this boundary is a point of contention among those who chronicle California bird records. However, without a firmly established southern boundary, latitude and longitude coordinates for sightings in the text, and an adequate map, the reader is unable to piece together patterns of pelagic bird distribution beyond Monterey Bay. A perfunctory conservation section confirms the threat of pesticides and habitat loss and lists the established habitat preserves. Phone numbers for two very helpful bird-alert hotlines are given as well as information on boat charters for pelagic birding.

What makes this book valuable to birders from outside Monterey County are the 10 detailed birding routes, most of which cover the more lucrative northern and western portions of the county. Whereas the trip maps are less than adequate, the directions and mileages

are good, and with a county map in hand, there should be no problems getting to the described areas. Trip times are not given, and fees for entering or passing through state parks and beaches would have been helpful.

The Species Accounts comprise 70% of the book and contain information compiled through December 1984 (with extended coverage for several species through September 1985). The terse and dry delivery is relieved by the small but good quality color plates. Each account includes a temporal bar graph and discussions of seasonal occupancy, habitat preference, and abundance. Subspecific designations are offered for 19% of the species. These were apparently extracted from computer printouts of specimen holdings at the Museum of Vertebrate Zoology, University of California, Berkeley, and do not reflect a rigorous personal evaluation. Whether subspecific designations have been assigned to sight observations is sometimes unclear. Roberson frequently associates subspecies with color shades—a misleading use of the subspecies concept. A 2.5 × 2.5-in. county map accompanies each breeding species account. It seems that the author was conscientious in showing distribution disjunctions, but without a detailed knowledge of Monterey County birds, I cannot comment on this. The author cited helpful articles (129 in all) for species he felt were poorly described in field guides. The bar graphs are consistent with the text with respect to timing and abundance, and all bar graphs are conveniently repeated as a group at the end of the book. Typographical and editing errors are occasional. A larger, more detailed topographic map would have eliminated some of the frustration I encountered in locating sightings mentioned in the text.

There is no doubt that regional faunal works are still needed. The value of a particular work depends upon the quality of documentation and how well it stimulates further field investigation. To his credit, Roberson has harnessed the vast and often ignored resource of birders' field notes. But incomplete gathering of hard data from museum study skins (only one of five important southern California collections is cited) and no reference to egg set holdings weakens the attempt to document historical patterns. Roberson fails to present the curious cases of distribution and abundance in an intriguing light. This could have been done by pointing out anomalous distributions or migration times relative to those from other parts of a species' range or by placing question marks on the range maps where work is most needed. "Monterey Birds" is an important synthesis of many data to which Roberson has special access as chairman of the California Bird Records Committee. Because his identification criteria are those of the Committee, this work is as rigorous as can be expected when dealing with sight records. Ideal for visitors to the area, this is a work that any student of the complex and fascinating patterns of west coast bird distribution will need to own.—MARK A. HOLMGREN.

HARRIER: HAWK OF THE MARSHES. By Frances Hamerstrom, illus. by Jonathan Wilde and Frederick Hamerstrom. Smithsonian Institution Press, Washington, D.C., 1986: 171 pp., 23 black-and-white sketches, 22 black-and-white photos, 18 figs., 11 tables. $24.95 (cloth), $10.95 (paper).—This is a very personal book. Although 12 appendixes contain considerable original data (pesticide levels in 45 harriers, breeding performance in relation to mating system, etc.), the brief episodic narrative (22 chapters, prologue, and epilogue average less than six pages each) is not so much a report on harrier breeding biology as it is a detailed accounting of how and why the author's 25-year study was conducted at all.

Hamerstrom's largely self-funded study of the breeding ecology of Northern Harriers (*Circus cyaneus*) on the 50,000-acre Buena Vista Marsh in central Wisconsin was truly a monumental effort (326 nests found, 647 nestlings banded, many adults individually marked

with imped feathers and color jesses). Reading this account only reinforces my impression of the urgent need for such science. Studies of this magnitude are an all too rare commodity.

Although Hamerstrom initiated the study in hopes of answering the "simple" question "Do harriers mate for life?" (they do not), the length of her study allowed her to do much more. For example, she documented both a decline in nesting during a period of widespread aerial application of DDT, and a subsequent increase in nesting after application of the pesticide was halted. Hamerstrom was assisted in the field by her husband, as well as an army of 48 "gabboon" volunteers. She graciously dedicates the book to them, and acknowledges their contributions throughout the work.

Hamerstrom's narrative very much succeeds in capturing the flavor of harrier research on the Buena Vista Marsh, but a book of this length, even if written in telegraphic "journal" prose (it is not), can offer but a glimpse at her heroic study. Readers wanting to know more about harriers, both on the author's study site and elsewhere, will need to consult the references cited in the text. The book is profusely illustrated with over 60 sketches, photographs, maps, and graphs, but, unfortunately, none of these is numbered, and many have only brief legends. As a result, at least some of the information available therein will be lost to the reader.—K.L.B.

THE OXFORD DICTIONARY OF NATURAL HISTORY. By Michael Allaby (ed.). Oxford Univ. Press, New York, New York, 1985:688 pp. $29.95.—Webster's Ninth New Collegiate Dictionary (1983) defines a dictionary as "a reference book containing words usually alphabetically arranged along with information about their forms, pronunciations, functions, etymologies, meanings, and syntactical and idiomatic uses." "The Oxford Dictionary of Natural History" fails to achieve this definition on two counts: it contains neither pronunciations, nor, except in a few rare instances, etymologies for the 12,000 entries it describes. There are no illusrations in the book (the dust cover illustrates two organisms that are not defined in the text!), nor are there any tables.

Although the flyleaf credits the work to a "team" of specialists under the direction of Michael Allaby, several entries left me wondering just how much teamwork occurred. For example, "isogamy," which is noted as being uncommon, is listed, but the presumably more common condition of anisogamy is not mentioned, let alone defined. Although mammalian anatomical features (homiothermic, four-chambered heart, hair, milk, etc.) are spelled out nicely under "mammalia"; the definition for "Aves" fails to include any anatomical characteristics, not even feathers! Many of the behavioral entries, with which I am most familiar, are fuzzy at best and include far too many errors of omission. There are also significant errors of commission in many entries, including the archaic definition of "interphase" as "the resting phase of the nucleus between succeeding mitoses."

More than half of the text is devoted to taxonomy, but it too has problems. For example, the entry "egrets" refers the reader to "*Egretta,*" which, although it defines the genus nicely, fails to mention that other genera of egrets exist. Similarly, the entry for "night-herons" refers the reader only to "*Nycticorax.*"

The book includes 75% of the 67 different items eight colleagues I queried suggested in their lists of 10 items that should be included. Most of the terms that were not included are new, and probably ephemeral, jargon; notable exceptions include "colonization," "population," and "survivorship."

Although my comments are highly critical, the book is overwhelmingly correct as written, and it does provide a listing of plant and animal taxonomy to the family level. Nevertheless, there are far too many problems with this "invaluable" "general reference" (the publisher's

words, not mine) for me to recommend it as an important addition to an ornithologist's reference shelf.—K.L.B.

THE FALL OF A SPARROW. By Sálim Ali. Oxford Univ. Press, Delhi, India, 1985:265 pp., 71 black-and-white photos, facs., letters, appendices, glossary. $16.95.—Sálim Ali, now in his 90th year, spans the entire history of ornithology and ecology as we know it today. How fortunate he has been to be part of the progress. As a child he grew up in a Muslim family in Bombay, India, which was closely knit (many members married cousins), prolific, interesting, vigorous, and deeply involved for centuries in trade and commerce from Hyderabad west to the Coast, and east to Burma, Malaysia, and Japan. Gregarious and enterprising, in business and the profession of the law, the family was notably above the divisiveness of religious partisanship, the historic bane of the Subcontinent.

Sálim Ali came to his interest in birds as a childhood hobby, keeping small birds in the kitchen garden of their compound, aided by small cousins and the clandestine help of the family cook. From here he went on during his school days and at college with an interest in sport and the out-of-doors. Gradually becoming aware of his abiding interest in nature and wildlife and forsaking all hope of a realistic business career, he left an attempt at pursuing money-making as a partner in an unsuccessful family commercial firm in southern Burma in 1917 and again, finally, in 1923, to resume a brief spell at St. Xavier's College in Bombay, finishing up a Bachelor of Science degree. In the meantime, his sojourn in Bombay had produced an engagement and marriage to a perfect wife, for him a companion and helpmeet in the field and abroad, Tehmina Latif. Tehmina must have been the light of his life, for Sálim Ali describes her transition from a sheltered childhood with a finishing school in England thrown in, to a sturdy, uncomplaining companion on trips by bullock cart into the jungles of an earlier India, who could make overnight camps in hut or bivouac liveable while subsisting on the inevitable rice and "dal" (dried split peas). Tehmina tragically died in 1939 of blood poisoning. The change in Ali's life must have been an incredible wrench.

In 1929 the Bombay Natural History Society commissioned Sálim Ali to visit Berlin to work for a year with Professor Erwin Stresemann, the leading authority on ornithology in Europe, one of the successful museum protagonists of *biological* ornithology who set the path towards closing the "yawning gap," as Sálim Ali describes it, between systematics and biology. This was a fortunate choice indeed, for here he met and worked with Oskar Heinroth, one of the fathers of ethology; Professor Rudolph Drost, pioneer bird ringer of Heligoland Island fame; and younger men such as Bernhard Rensch. This trip to Germany was partly inspired by the current ferment in India over nationalism and the Congress movement and the actual or assumed sense of paternalistic snobbery emanating from the British Museum. On his return to India he began working closely with the Bombay Society, soon becoming Honorary Editor of the esteemed journal of the Society, as well as a field collector and research director. It was in this year that Sálim Ali was commissioned by the Society to collect notes and brief descriptions to produce finally, in 1941, *The Book of Indian Birds,* which listed some 180 bird species, including brief description, field identification, distribution, habits, food, calls and nesting, and color illustrations, including also a few general chapters on migration, flight, bird watching, utility of birds to man, in sum the ushering in of India to the "world of Peterson" as we Americans might describe it. (I can remember seeing the book on sale in railway station stands along with "Penguins" during the war.) The book was an instant success, went into eleven editions, and no doubt was greatly helped by its publication during the years of World War II. India, up to then not a well-known tourist haunt, of course had been invaded by hordes of foreign troops, mostly British, thus

starting the train of circumstances that has resulted in a continuing stream of books by this wonderfully talented author and spokesman for natural history.

Although Sálim Ali's books and definitive natural history survey volumes on regions of India have continued to come out in a steady progression, it is perhaps as a technical writer in the field of ecology that his personal satisfaction resides. His monograph on the weaver birds delineated the life history, nesting behavior, and courtship of these sparrow-relatives in as comprehensive and authoritative terms as our own Margaret Nice on Song Sparrows (*Melospiza melodia*). His observations in the field have helped to illuminate the monumental 10-volume *Handbook* series, 1968–74, and extend its boundaries beyond description and into the realm of original observation.

In the end Sálim Ali will be known as one who successfully opened the eyes of the population of the Indian Subcontinent to the present dangers threatening their environment. It is a fascinating progression from his initial love of birds as a subject, through a study of the history of the Moghul Emperors and their hunting exploits which revealed—in the manner of the reading of diaries of the Asian Courts—the change and inherent decline of the original environment, on through bird study, not only to ethology and behavior, but also patient encyclopedic knowledge. Finally all this leads to the present ferment on conservation and environmental control. In his continual teaching, and his constant search for knowledge, he has given special meaning to the world of ornithology, a higher, larger meaning implicit with a lesson for the welfare of mankind. Thus the essential value of this extraordinary story of one man's journey to enlightenment.—S. Dillon Ripley.

A Guide to Bird Finding in New Jersey. By William J. Boyle, Jr., illus. by David A. Sibley. Rutgers Univ. Press, New Brunswick, New Jersey, 1986:512 pp., 10 bird drawings with captions, 77 maps. $19.95.—A good guide to birding in New Jersey has been a desideratum for some time. With existing guides and books on the Delaware Valley, South Jersey, the New York City region including North Jersey, and site guides scattered abundantly over various magazines (Birding, Records of New Jersey Birds), birders had to accumulate fragmented information that was hard to use. Now birders have all that information in one place, and a wealth of useful information it is, with sections on birding by season, rare bird alerts (4 cover New Jersey), birding ethics, general precautions, birding spots organized by region (all the best with maps), pelagic trips, hawk-watching, and nature clubs and Audubon chapters. A bibliography, index, and an annotated list of the state's regularly occurring birds are also included.

The book is divided into six sections by state birding regions (the regions bounded by major highways) indicated in Map 1 (Northeast, Northwest, Central, North Coast, South Coast, Southwest). Each section is prefaced with a regional map showing counties and main roads. The birding places are numbered on the regional maps, making location easy. Each major birding location (77 from High Point to Cape May) has a clear set of directions, a good map by the author (from experience), and a section on birding the area (i.e., how, when, and what to look for). Generally the seasons are treated thoroughly. Both common and rare species are noted for birding locales (not always well done in birding guides but well done here). At the end of each regional section are briefer accounts of additional birding spots without maps but with concise directions. The virtue of these additions is that they will stimulate more investigation of these lesser-known areas, like Beaver Swamp in Cape May County (p. 431). Although New Jersey is one of the most thoroughly birded (and reported) states in the country (what with four alerts, Records of New Jersey Birds, Cassinia, numerous books, including those by Stone, Bull, Fables, and Leck), and although it has

Brigantine, Princeton, and Cape May, it still has hidden places that need to be explored. Directions to birding spots were frequently field-tested and birding accounts reviewed by the local birder most familiar with the area before printing. This shows in the end product, a meticulous account of the best places in the state. Very little information is omitted from the birding area accounts. The author is already gathering information on the inevitable road closings, gate closings, etc. since publication, against a possible updating for a second printing, further testimony to the thorough work done in the writing.

This guide will prove most useful to out-of-staters and out-of-country birders as well as to experienced resident birders seeking to know the state better, to researchers looking for study areas, to beginning birders seeking to learn where to go and how to bird, to big day birders planning a route, to seasonal and once-a-year birders, and to backyard birders. The section on Nature Clubs provides a list of local birding contacts, and the bibliography provides sufficient references for understanding the status of New Jersey birds and their distribution. The annotated checklist of New Jersey's birds (45 pp. and 360 regularly occurring species) is especially valuable for birders or researchers looking to find a particular species. The probability ratings (borrowed from the Lane guides) are geared to the birder's desire to know the likelihood of encounter, not necessarily to true abundance (i.e., "Hard to miss," "Should see," "May see," "Lucky to find," "How lucky can you get"). Caution: the annotated checklist should not be read as an exhaustive description of species distribution; in most entries only a few locations are listed, usually the more famous ones. This caveat aside, the checklist does answer the basic birder questions: when and where in New Jersey, and what are my chances?

Pelagic birders and the hawk-watching fraternity will delight in the special sections devoted to their respective addictions. The shorebird buffs will perhaps resent the absence of a special section (possibly deserved in a New Jersey guide), but, on the other hand, one hears no clamorous groundswell of partisan support for "fringillid-watching" or "flycatcher trips." The hawk-watching and pelagic sections will be very helpful to new birders and out-of-staters who do not have these opportunities in their own backyards. The introduction and the sections on birding precautions, how to use the book, and common species are clear and concise. The index is very comprehensive. The birding ethics section (an increasing preoccupation these days) is perhaps too brief to be inclusive or to treat adequately the questions it raises. For instance, secrecy about raptor nests may be desirable to fend off undesirables (kids with bow and arrow, etc.), but published information is also useful in getting areas protected or heading off habitat alterations. This is a two-edged question requiring further elucidation. Moreover, should owl roosts be reported on bird alerts? Also, should private property birds be on rare bird alerts? Should endangered species? The comments on overuse of tape recorders are welcome. Elimination of tapes on big days when scores of birders are afield in the same locales is a conclusion one might draw from what the author has to say. Although the treatment is too cursory, the author is to be congratulated for avoiding pomposity, often the salient feature of birding ethicist monologues.

The drawings are attractive and the selection of species quite appropriate for New Jersey. There are not too many of them; restraint was exercised against the tendency to over-illustrate. The Barred Owl (*Strix varia*) cover design is appealing, but the quality and durability of the cover material is less than satisfactory; other choices were available, covers for instance that are still flexible but of the same durability and quality of the covers on the new Peterson "Field Guide to the Birds East of the Rockies" or the Sierra Club Guides to the National Parks. Perhaps holding down the price was a concern; the cover undoubtedly will help resales or argue for a reprinting with updates. In brief, the book is a necessity for anyone interested in New Jersey birds.—RICHARD KANE.

TALES OF A LOW-RENT BIRDER. By Pete Dunne, illus. by David Sibley. Rutgers Univ. Press, New Brunswick, New Jersey, 1986:xvi + 157 pp. $15.95.—This book collects 19 short essays or stories originally published in the "Peregrine Observer," the newsletter of the Cape May Bird Observatory, during the last 9 or 10 years. Most concern, at least marginally, Cape May, New Jersey, where Dunne was Director of the Observatory. They range from musings on encounters with birds and bird-watchers, to accounts from the bird's point of view, to satires (at least one of them quite bitter) on future trends in birding. Almost all show a deep concern for conservation; a love of all nature and birds in particular; and a tolerance for people, even those who share neither his concern nor his love. Dunne has a very informal, relaxed, and easy (for the reader, not, I am sure, for the writer) style of writing that makes these collected works seem more like quiet conversations with an old friend than formal essays. Anyone sharing his enthusiasm for birds and birding should find this book good, satisfying, even inspiring, fun. Certainly it makes me want to get back to Cape May as soon as possible.—THOMAS S. PARSONS.

BIRDS WORTH WATCHING. By George Miksch Sutton. Univ. Oklahoma Press, Norman, Oklahoma, 1986:xv + 205 pp., 60 color photographs. $19.95.—During his long and productive career, George Sutton wrote 14 books, all of which were characterized by lucid prose, an entertaining style, and a knowledgeable and sympathetic treatment of birdlife. This final work consists of short essays averaging about two and one half pages each, covering about 60 selected bird species. Most of these are widespread common species, but a few have restricted ranges. In his usual style, Dr. Sutton relates some rather personal experiences with these species, together with observations obtained from a host of his students and friends. Frequently the observation involves a behavior that puzzled Sutton at the time and for which he may or may not have ultimately gained an explanation. The latter part of most of these essays, indeed, consists of several questions or suggestions for minor research projects. Is the Carolina Wren (*Thryothorus ludovicianus*) susceptible to winter kill because it is lightly feathered? Does the female Downy Woodpecker (*Picoides pubescens*) drum? Where do adult male Hooded Mergansers (*Lophodytes cucullatus*) spend their eclipse period? How do Chuck-Will's-Widows (*Caprimulgus carolinensis*) catch small birds, as they are known to do? I suspect that few of these intriguing questions will attract the new graduate student seeking a thesis title, but rather they should tickle the curiosity of the amateur anxious to make a contribution.

But besides the puzzling questions, there is a lot of information about these common species that can be learned from reading "Doc's" last book. As might be expected, many of these observations were made during the author's long residence in Oklahoma, particularly his favorite Black Mesa country, but other areas of the country are not neglected.

This book will, however, bear one distinction for a Sutton book. To my knowledge it is the only one not illustrated by the author's beautiful paintings. For each species there is an attractive color photograph. These were collected from several sources by John S. Shackford, who indeed took many of them.

There is a fine Foreword by Olin Sewall Pettingill Jr., George Sutton's longtime friend. Sutton's many friends will cherish this last work, and I recommend it highly to those who did not know the man except by repute.—GEORGE A. HALL.

ALSO RECEIVED

THE NEW WHERE TO WATCH BIRDS. By John Gooders. Andre Deutsch, London, England. (Distributed by David & Charles, North Pomfret, Vermont 05053), 1986:224 pp., many maps. $17.95.—This is essentially the third edition of Mr. Gooders' guide to birdfinding in Great Britain. The island is divided into 14 regions, and numerous areas (each rated by a star system) are included in each. Full directions for reaching the best sites, often with a map, are given together with a list of birds to be seen at various seasons. American birders, used to birding almost anyplace, will upon their first trip to Britain be dismayed by the fact that most of the countryside is unavailable to them. Mr. Gooders' book, which largely discusses reserves and sanctuaries where birding is possible, will be of great use to such visitors. The Preface will also give Americans an inkling of what the conditions for bird watching now prevailing in Britain are like. A "Code for the Bird Watcher" is included.—G.A.H.

BIRD SEEKERS GUIDE. By John Gooders. Andre Deutsch, London, England. (distributed by David & Charles, North Pomfret, Vermont 05053), 1985:208 pp, 21 black-and-white photos. $6.95 (paper).—This is a reprint of a 1980 publication that attempts to give directions for finding specific species of British birds. As such it is a possible companion of the book in the previous review. For each species a statement of general status, a summary of habitat, and some suggestions as to where to find it are given.—G.A.H.

THE BIRDS OF THE CRESTON VALLEY AND SOUTHEASTERN BRITISH COLUMBIA. By Robert W. Butler, Brian G. Stushnoff, and Edward McMackin. Canadian Wildlife Service Occasional Paper No. 58, Environment Canada, Ottawa, K1A 0E7, Canada, 1986:37 pp., 14 black-and-white photos, maps, and graphs. Free from the publisher.—An annotated list of 250 species recorded in the Creston Valley Wildlife Management Area of which 147 are known or highly suspected of breeding. Quantitative data indicate that waterfowl broods have increased fivefold since 1966 and that landbirds have also increased.—G.A.H.

POPULATION ECOLOGY OF MIGRATORY DUCKS IN LATVIA. By H. Mihelsons, A. Mednis, and P. Blums. Latvian SSR Academy of Sciences, Inst. of Biology, Riga, U.S.S.R. (Zinatne Publishing House), 1986:111 pp. No price given.—In Russian with English summary.—G.A.H.

CHANGE IN EDITOR

Dr. Charles R. Blem will serve as Editor of *The Wilson Bulletin* beginning with Volume 100. All manuscripts submitted for publication in the *Bulletin* should be sent to him at the Department of Biology, 816 Park Avenue, Virginia Commonwealth University, Richmond, Virginia 23284. All manuscripts received prior to 1 May 1987 will continue to be processed by Keith L. Bildstein.

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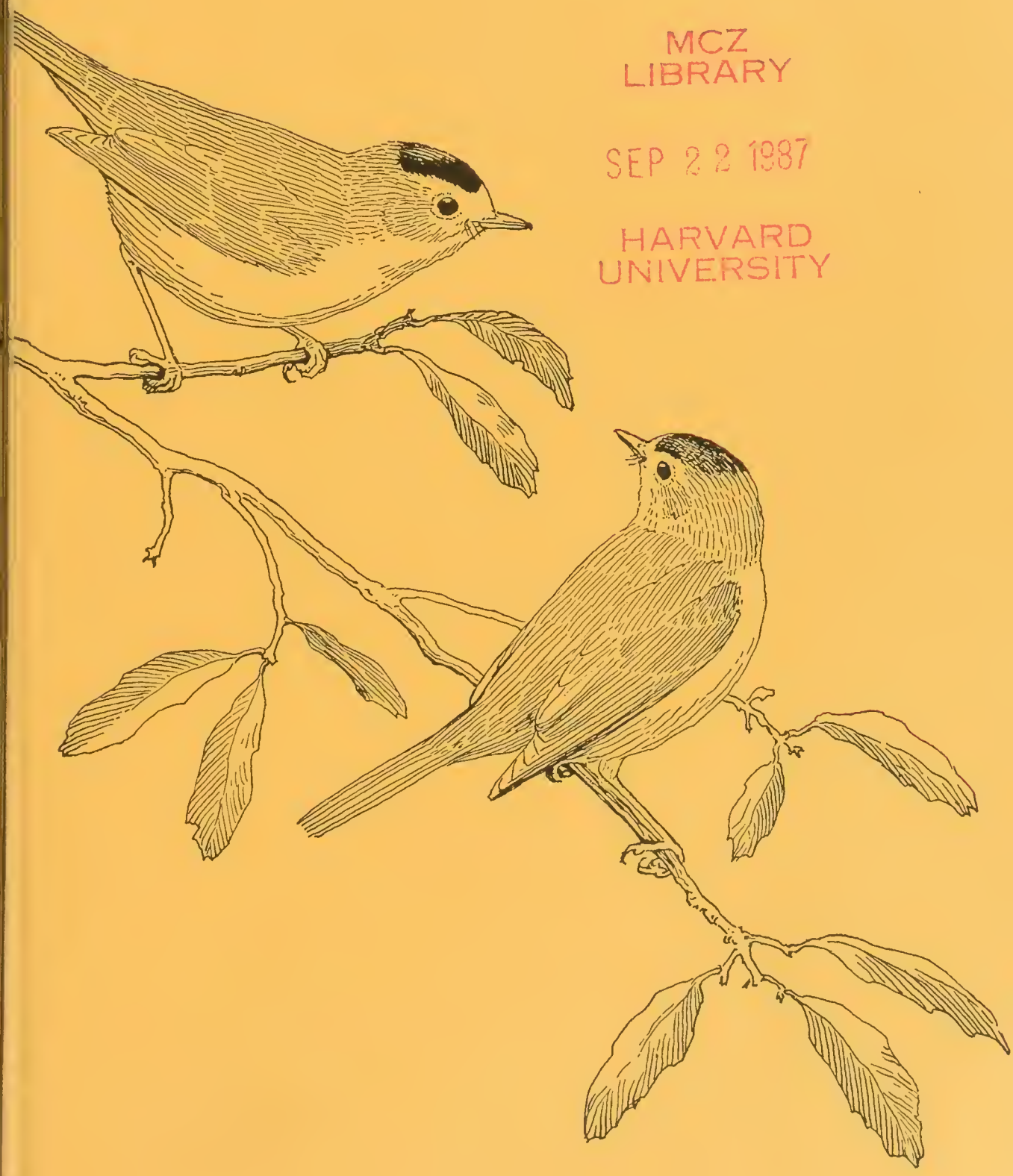

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Two small rufous sympatric Peruvian antpittas of the genus *Grallaria*, *G. blakei*, sp. nov. (upper) and *G. rufula* (lower) from a mixed media painting by John P. O'Neill.

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A CRYPTIC NEW SPECIES OF ANTPITTA (FORMICARIIDAE: *GRALLARIA*) FROM THE PERUVIAN ANDES

GARY R. GRAVES[1]

ABSTRACT.—Two morphologically similar antpittas, *Grallaria rufula* and *G. blakei*, sp. nov., are sympatric on Cordillera Colan and Cordillera Carpish in the Peruvian Andes. These taxa appear to replace one another elevationally: *G. rufula*—2590 to 3450 m; *G. blakei*—2135 to 2470 m. *G. blakei* differs from Peruvian populations of *G. rufula* in having barring on the lower belly and much darker reddish-brown plumage. A unique specimen from the geographically isolated Cordillera Yanachaga may represent an undescribed subspecies of *G. rufula* or *G. blakei*, or an undescribed third species. *Received 30 June 1986, accepted 7 Nov. 1986.*

Four or more antpitta species of the genus *Grallaria* occur along an elevational gradient at nearly every humid forest locality in the main chain of the Andes from Venezuela and Colombia south to northern Bolivia. Up to eight species have been collected along an elevational gradient in the Central Cordillera of the Colombian Andes. In this region and others, the morphological distinction between sympatric species has been clear-cut. The only taxonomic difficulty regularly encountered has been deciding the status of allopatric taxa (e.g., Schulenberg and Williams 1982).

Here I report an exception to previously known patterns in the genus. Two morphologically similar antpittas occur sympatrically in at least two localities along the forested Amazonian slope of the Eastern Andes in Peru. One of these taxa is *Grallaria rufula*, a widespread, polytypic, high-elevation (2300–3350 m) species. The other taxon represents an undescribed cryptic species with a more restricted geographic distribution and

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lower altitudinal range (2135–2470 m). Specimens of the new species were first collected in the Cordillera Carpish, Department of Huánuco, in the 1960s. Although Tallman (1974) incorrectly identified these as *Grallaria rufula obscura,* he noted that they were larger and darker than specimens of *G. rufula* collected at higher elevations and suggested that two biological species were involved.

Populations of the new species are easily separated by plumage from Peruvian and Bolivian populations of *G. rufula*; however, some specimens of *G. rufula* from western Colombia are more similar in overall appearance to the new species than they are to Peruvian and Bolivian populations of *G. rufula.* To determine to which taxon the Colombian birds can be assigned, I revised *G. rufula* on the basis of morphology, plumage, and elevational distribution (Graves, in prep.). This preliminary study indicated that the Colombian birds represent an undescribed taxon, presumably a subspecies of *G. rufula,* and that the new species is apparently restricted to Peru. In this paper I focus on the most easily resolvable systematic issue—the discrimination of sympatric species in the Peruvian Andes.

Grallaria blakei, sp. nov.

CHESTNUT ANTPITTA

HOLOTYPE.—Louisiana State University Museum of Zoology No. 64228; adult female from the east slope of the Cordillera Carpish, near the Carretera Central, ca 2400 m, Department of Huánuco, Peru; collected 17 August 1968 by John P. O'Neill; original number 3292.

DIAGNOSIS.—*Grallaria blakei* is similar to *Grallaria rufula* in color of plumage and size and shape, but may be distinguished from all populations of *G. rufula* by possessing the following combination of characters: dark reddish-brown dorsum, head, and breast, without contrasting feather tips (clay colored [*G. r. saltuensis*] to dark brown in *G. rufula*); indistinct barring on feathers of lower belly (unmarked or with teardrop shaped markings in *G. rufula*); dark brown undertail coverts (white to dark brown in *G. rufula*); thicker bill and tarsi; and by lacking a contrasting eyering or prominent central stripes on flank feathers.

DESCRIPTION OF HOLOTYPE.—All color comparisons were made under Examolites® (Macbeth Corp.). The crown, nape, back, scapulars, wings, rump and tail are uniform brown; averaging Chestnut (capitalized color names are from Ridgway 1912), and brightening to Burnt Sienna on the preocular region, orbital feathers, auriculars, throat, and breast; and merging into Cinnamon-Brown and then Prout's Brown on the flanks, thighs, and undertail coverts. The center of the lower belly is light buffy-gray; the outer portion of the feathers banded with indistinct darker gray bars. Soft part colors in life: bill black, iris brown, feet and tarsi slate.

MEASUREMENTS OF HOLOTYPE (mm).—Wing chord, 78.5; bill length (from anterior edge of nostril), 11.0; bill width (anterior edge of nostril), 5.4; tarsus length, 38.0; narrowest medio-lateral width of tarsus, 1.6; middle toe length (sum of outer two phalanges and claw), 21.8.

DISTRIBUTION.—Known from three localities (Fig. 1) in the Eastern Andes of Peru: (1) the north-facing slope of the Cordillera Carpish, below Carpish Pass, Department of

FIG. 1. Speeimen localities for *Grallaria blakei* (A, B) and species indeterminate (C) in humid forest (ca 1200–3400 m) along the eastern slope of the Peruvian Andes. A. Specimens eollected NE Florida and on Cordillera Colán, Dpto. Amazonas. B. Cordillera Carpish, Dpto. Huánuco. C. Cumbre de Ollón, Dpto. Pasco. Adapted from Graves (1985).

Huánuco, 2135–2400 m (FMNH No. 275632; LSUMZ Nos. 64228, 74096, 74098, 75098, 75243); (2) Cordillera Colán, SE La Peca, Department of Amazonas, 8100 ft (2470 m) (LSUMZ No. 88068); and (3) 30 (road) km NE Florida, Department of Amazonas, 2200 m (LSUMZ No. 116973). Probably occurs more or less throughout the intervening area.

SPECIMENS EXAMINED.—*G. rufula*: Colombia: (by mountain range and department): Sierra Nevada de Santa Marta—Magdalena (CM 1 ♂, 2 ♀♀; USNM 1 ♂, 2 ♀♀). Serranía de Perijá—La Guajira/Cesar (USNM 2 ♂♂, 2 ♀♀). Eastern Cordillera—Norte de Santander (FMNH 2 ♂♂); Santander/Boyaeá (CM 2 ♂♂; USNM 1 ♂, 1 ♀); Cundinamarca (AMNH 2 ♂♂). Central Cordillera—Risaralda/Quindío (AMNH 3 ♂♂); Cauca (ANSP 1 ♀; FMNH 2 ♂♂); Nariño (ANSP 1 ♂, 1 ♀; FMNH 1 ♀). Western Cordillera—Antioquia (AMNH 1 ♀; USNM 1 ♀); Cauca (AMNH 1 ♀; LACM 1 ♀).

Ecuador: (AMNH 11 ♂♂, 4 ♀♀; ANSP 2 ♂♂, 1 ♀; LSUMZ 1 ♂; UMMZ 1 ♂; MVZ 2 ♂♂, 1 ♀; MLOC 1 ♂).

Peru: (by department): Piura/Cajamarca (AMNH 2 ♂♂, 1 ♀; LSUMZ 3 ♂♂, 5 ♀♀; USNM 1 ♂). Amazonas (LSUMZ 8 ♂♂, 3 ♀♀). San Martín/La Libertad (LSUMZ 1 ♂, 6 ♀♀). Huánuco (north of Río Huallaga) (ANSP 1 ♂, 1 ♀; FMNH 2 ♂♂, 1 ♀; LSUMZ 5 ♂♂, 4 ♀♀). Huánuco (south of Río Huallaga)/Pasco (FMNH 1 ♀; LSUMZ 11 ♂♂, 14 ♀♀). Junín/Ayacucho (AMNH 3 ♂♂, 1 ♀; LSUMZ 2 ♂♂, 4 ♀♀). Cuzco (AMNH 1 ♀; FMNH 2 ♀♀; LSUMZ 5 ♂♂, 2 ♀♀; USNM 3 ♂♂, 3 ♀♀). Puno (LSUMZ 3 ♂♂, 5 ♀♀).

Bolivia: (by department): La Paz (LSUMZ 7 ♂♂, 3 ♀♀). Cochabamba (ANSP 1 ♀; CM 1 ♂; DMNH 1 ♀; LSUMZ 6 ♂♂, 6 ♀♀).

Species indeterminate: Peru: Cumbre de Ollón, Dpto. Pasco (LSUMZ 1 ♀).

ETYMOLOGY.—I take great pleasure in naming this new species for Emmet Reid Blake of the Field Museum of Natural History for his many significant contributions to our knowledge of the systematics, taxonomy, and biogeography of Neotropical birds.

DISCUSSION

Plumage variation.—There is no consistent sexual difference in plumage among the Carpish specimens of *Grallaria blakei.* One specimen (LSUMZ No. 74098 ♂, 2 August) has traces of streaked juvenal plumage scattered over the head, nape, throat, wing coverts, and breast. Another (LSUMZ No. 75243 ♂, 22 November) has a few juvenal feathers on the hind crown. The characteristic barring on the lower belly of adult *G. blakei* is present in both of these specimens.

Two specimens from the Department of Amazonas (Cordillera Colán, LSUMZ No. 88068 ♀; NE Florida LSUMZ No. 116973 ♀) differ from those of the type locality in having brighter underparts and less distinct barring on the lower belly. Montane forest is nearly continuous along the Amazonian slope of the Eastern Andes from the Río Marañón south to the Huallaga canyon; thus, these populations are probably in direct genetic contact. Were it not for this hypothesized, but unproven, cline in plumage characters, the Amazonas population could be validly described as a new subspecies.

A single specimen (LSUMZ No. 106081, ♀; wing chord, 79.8; culmen length, 11.2; bill width, 5.2; tarsus length, 39.9; tarsus width, 1.6; middle toe, 24.6) recently collected at 2500 m on Cumbre de Ollón, ca 12 km east of Oxapampa, Department of Pasco, may represent an undescribed subspecies of either *G. blakei* or *G. rufula,* or perhaps an undescribed third species. It is darker above than any of the known populations in the *rufula-blakei* species complex and lacks the ventral markings characteristic of *G. blakei.* Cumbre de Ollón is near the summit of the Cordillera Yanachaga, an outlying range separated from the main Andes by the Río Santa Cruz Valley (Schulenberg et al. 1984). T. Schulenberg (in litt.) recorded a single-noted call (song?) which he believed was given by the same taxon collected earlier by D. Wiedenfeld. Both Schulenberg and T.

Parker indicate that this vocalization was unlike that given by any population of *G. rufula* known to them. As unequivocal *G. rufula* was neither seen, netted, nor heard in this locality, the "rufous" population of *Grallaria* in the Cordillera Yanachaga is apparently an allopatric isolate. Although I suspect that this population is closely allied with *G. blakei,* more data are needed for a definitive analysis and taxonomic description.

A skeletal specimen (LSUMZ 70234) identified as *G. rufula* was collected at Ccarapa (2485 m), on the road from Tambo to the Río Apurímac, Department of Ayacucho, approximately 300 km southeast of the Cordillera Yanachaga. Along the same road, Weske (1972) recorded *G. rufula* from 3000 to 3600 m. Because of the robustness of the cleaned maxilla (bill width = 4.7 mm) and tarsometatarsus (tarsus width = 1.5 mm) and low elevation of collection, I suspect that this specimen represents the same taxon as the Cordillera Yanachaga specimen or perhaps *G. blakei.* Unfortunately, the individual was not fully adult (incompletely ossified ends of the long bones) and could not be compared profitably with the few available skeletons of *G. rufula.*

The two specimens taken south of the Río Huallaga suggest that *G. blakei* and its allies have a latitudinal range of at least 900 km along the eastern slope of the Peruvian Andes.

Reproductive condition.—None of the adult specimens from the Cordillera Carpish was in reproductive condition (LSUMZ No. 74097 ♂, 10 August; FMNH No. 275632 ♂, 21 October; LSUMZ No. 64228 ♀ (type), 10 August; LSUMZ No. 74096 ♀, 12 August). The female collected NE Florida (29 November) had an enlarged ovary (10 × 8 mm) with 3 mm ova. These data, and the occurrence of individuals with traces of juvenal plumage in August and November, suggest that breeding may be seasonal, probably from December through April or May.

Vocalizations.—Although the vocalizations of *G. rufula* are relatively well known, those of *G. blakei* have not yet been identified. For example, no songs or calls attributable to either *G. blakei* or *G. rufula* are known from the lower part (<2500 m) of the Paty Trail in the Cordillera Carpish, where only *G. blakei* has been collected (T. Parker, pers. comm.). Attempts to identify the vocalizations of *G. blakei* should be given high priority.

Morphological variation.—Measurements of females and males of *G. blakei* overlap in our small series (Table 1). *G. blakei* is statistically distinguishable ($P \leq 0.05$) from sympatric populations of *G. rufula* in several morphological characters (e.g., bill length, tarsus length, bill width). In general, *G. blakei* appears to be slightly more robust than *G. rufula.* This is expressed in the significantly wider bill and thicker tarsus of *G. blakei.*

A representation of *G. blakei* and *G. rufula* in multivariate morphological space is shown in Fig. 2. Separate Principal Component Analyses

TABLE 1

RANGES AND MEANS (±SD) OF MEASUREMENTS OF SYMPATRIC POPULATIONS OF *G. RUFULA* (CORDILLERA COLÁN SOUTH THROUGH CORDILLERA CARPISH) AND *G. BLAKEI* (WITHIN EACH SEX, CHARACTER MEASUREMENTS OF EACH SPECIES WERE COMPARED WITH STUDENT'S *t*-TEST)

	Males		Females	
Characters	*rufula* (N = 16)	sp. nov. (N = 4)	*rufula* (N = 13)	sp. nov. (N = 4)
Wing chord	78.8–84.3 81.3 (1.7)	81.1–85.2 83.2 (1.8)	78.2–84.5 81.6 (1.5)	78.5–83.8 81.6 (2.3)
Culmen length[a]	10.0–12.1[d] 10.9 (0.5)	11.0–11.9 11.6 (0.4)	9.9–12.0 10.9 (0.6)	10.5–11.0 10.8 (0.2)
Bill width[a]	4.2–5.2[f] 4.8 (0.2)	5.3–5.6 5.5 (0.1)	4.2–5.2[e] 4.9 (0.3)	5.3–5.6 5.5 (0.1)
Tarsus length	40.2–43.6[d] 41.7 (1.0)	42.7–43.4 43.1 (0.3)	39.3–43.2 41.4 (1.3)	38.0–42.2 40.5 (1.8)
Tarsus width[b]	1.4–1.6[d] 1.5 (0.1)	1.5–1.8 1.6 (0.2)	1.4–1.6[e] 1.5 (0.1)	1.5–1.8 1.7 (0.1)
Middle toe[c]	20.9–23.7[e] 22.5 (0.9)	23.3–24.8 24.0 (0.6)	21.5–23.3 22.4 (0.5)	21.5–23.3 22.2 (0.8)

[a] Measured from anterior edge of nostril.
[b] Narrowest medio-lateral point on tarsometatarsus.
[c] Sum of outer two phalanges and claw.
[d] $P < 0.05$.
[e] $P < 0.01$.
[f] $P < 0.001$.

were performed on pooled groups of males (N = 80) and females (N = 66) (Table 2). In the plot of PCA scores for females, one sympatric *G. rufula* (LSUMZ 92475, Mashua, 3350 m, Dept. La Libertad) falls within the envelope outlined by the small sample of *G. blakei*. Although this specimen has a relatively thick bill (bill width = 5.0 mm) and tarsi (1.6 mm), the plumage shows no trend toward *G. blakei* in either color or pattern. Two specimens from allopatric populations in the Western Cordillera of Colombia (and the Cumbre de Ollón specimen) have high PCA I scores. They are very similar in external morphology to *G. blakei* but differ in several distinctive plumage characters and were collected at or above the upper elevational limit of that species (2400 and 3150 m). Nothing is known of these populations in life, and although I provisionally refer these to *G. rufula*, they may represent yet another undescribed species in the *rufula* complex. Males of *G. blakei* are relatively isolated from sympatric and allopatric populations of *G. rufula* in principal component space.

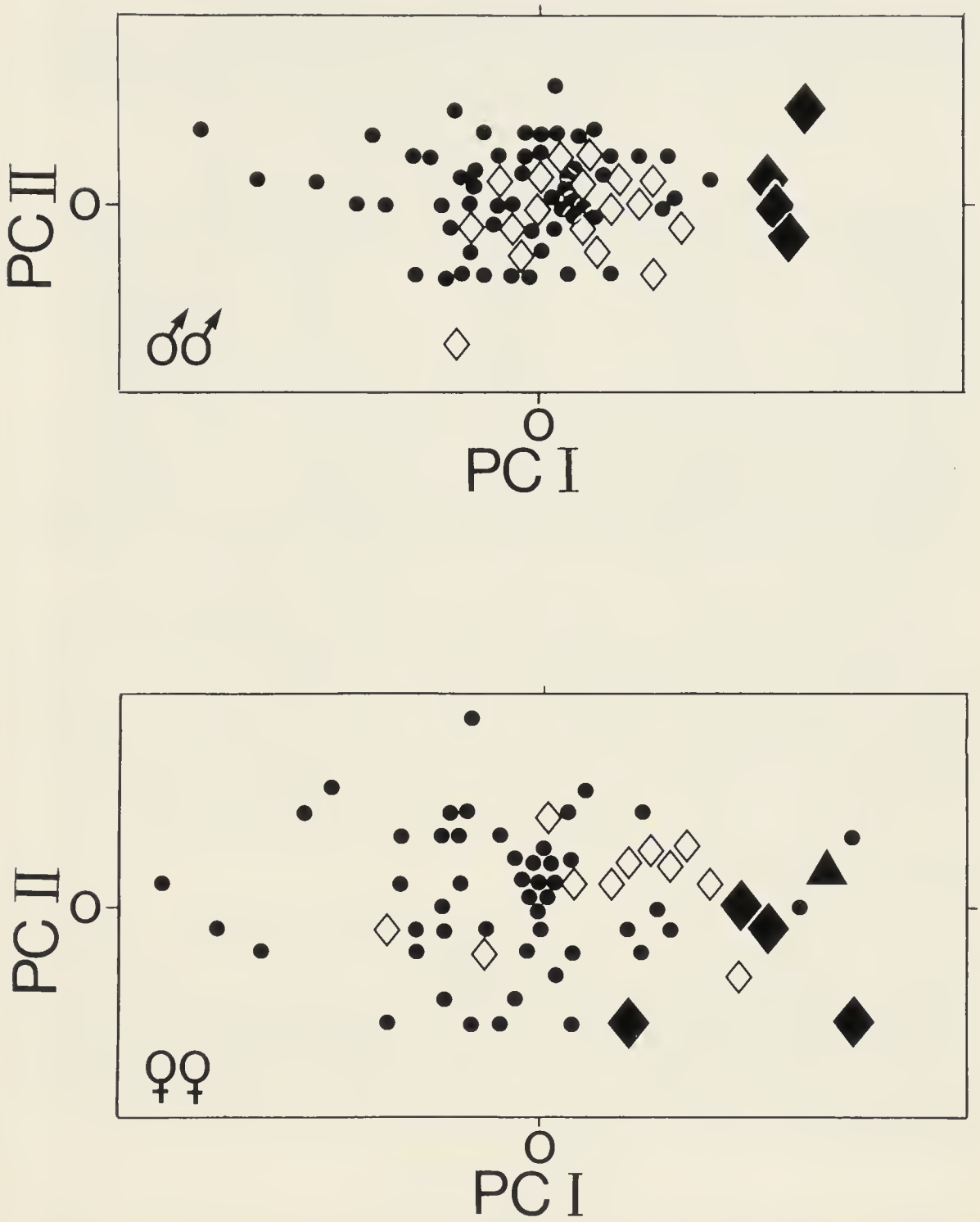

FIG. 2. Bivariate plots of factor scores for the first two unrotated principal components extracted from correlation matrices. Solid diamonds = *Grallaria blakei*. Solid triangle = species indeterminate from Cumbre de Ollón. Hollow diamonds = sympatric *G. rufula* (Cordillera Colán south to Cordillera Carpish). Solid circles = allopatric *G. rufula* (from localities beyond the known range of *G. blakei*).

TABLE 2
FACTOR LOADINGS FOR THE FIRST TWO PRINCIPAL COMPONENTS FROM SEPARATE ANALYSES OF MALES AND FEMALES

Variable	Males		Females	
	I	II	I	II
Wing chord	0.247	0.354	0.703	0.076
Bill length	0.706	0.327	0.446	−0.473
Bill width	0.771	0.194	0.808	−0.153
Tarsus	0.588	−0.606	0.388	0.785
Tarsus width	0.301	0.701	0.595	−0.457
Middle toe	0.708	−0.456	0.358	0.694
Variance explained				
Percent	38.9	22.3	33.0	26.0
Cumulative	38.9	61.2	33.0	59.0

Behavior and ecology.—All specimens of *G. blakei* have been netted or shot within 2 m of the forest floor in dense cloud forest. T. J. Davis noted that the stomach of one specimen (LSUMZ 116973) netted in "dense, stunted, humid forest" contained beetle remains. No other ecological information was recorded on specimen tags, and field observations have been limited to brief glimpses of individuals immediately before they were collected. As such, *G. blakei* is the most poorly known of the *Grallaria* species occurring in Peru.

In both localities where *G. blakei* and *G. rufula* are known to be sympatric, a distributional hiatus is found between their known elevational ranges: Cordillera Colán, *G. rufula*—2590 to 3290 m, *G. blakei*—2470 m; Cordillera Carpish, *G. rufula*—2740 to 3450 m, *G. blakei*—2135 to 2400 m. Whether this gap is real or an artifact of sampling is not known. Field parties should devote special effort to tape-recording the calls and collecting any "rufous" antpitta encountered below 2600 m.

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COLOR PLATE

The Frontispiece painting by John P. O'Neill has been made possible by an endowment established by George Miksch Sutton.

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BEHAVIORAL DIFFERENCES AMONG SEX AND AGE CLASSES OF THE BROWN-HEADED COWBIRD AND THEIR RELATION TO THE EFFICACY OF A CONTROL PROGRAM

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ABSTRACT.—The recent colonization of the Sierra Nevada by the Brown-headed Cowbird (*Molothrus ater*), a brood parasite, may constitute a threat to some passerine populations. Because radio-telemetry studies have demonstrated that cowbirds commute up to 7 km between breeding sites in natural habitats and man-made feeding sites such as pack stations (horse corrals), it seemed possible to control cowbirds over a large area by removing them from a small number of man-made feeding sites. The feasibility of such a control program was tested by removing 125 cowbirds from a pack station in the western Sierra Nevada. Although cowbird numbers at the removal site declined markedly, there was only a moderate decline in male cowbirds, and at best only a slight decline in female cowbirds in the general area surrounding the removal site. The removal program had a limited impact because many cowbirds in the area, especially females and adult males, often fed in the vicinity of cattle grazing in meadows, unlike cowbirds in the area where the radio-telemetry study was done. Because free-ranging cattle are widespread in the Sierra, short-term removal programs at localized sites may have limited value, except in the few areas where there are no free-ranging cattle. Our results indicate that cowbirds are highly attracted to horses and make only limited use of corrals in the absence of livestock. Yearling males spent more time at a social feeding site than did adult males and females which, along with other evidence, indicates that cowbirds form afternoon social groups for purposes of feeding, rather than to partake in social behavior in a lek-like situation. *Received 23 Aug. 1986, accepted 13 Feb. 1987.*

The phenomenal increase in the distribution and abundance of the Brown-headed Cowbird (*Molothrus ater*) over the last 200 years probably exceeds that of any other native North American bird (Mayfield 1965, Rothstein et al. 1980). Because the cowbird is a brood parasite, victimizing nearly all passerines with which it is sympatric (Friedmann 1963, Friedmann et al. 1977, Friedmann and Kiff 1985), its range extension may have placed a new and potentially serious limit to the reproductive potential of some host populations. Indeed, the cowbird has been implicated in the decline of both endangered and common species (Mayfield 1977, Brittingham and Temple 1983). We report on the efficacy of a possible control program thought to be especially well suited to the Sierra Nevada

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of California and other semiwilderness areas. We also describe behavioral differences among sex and age classes of cowbirds, as indicated by the results of intensive trapping. These behavioral differences are significant to studies of the behavioral ecology of the cowbird (see review in Rothstein et al. 1986) and to understanding shortcomings in the control program we tested.

The Sierra Nevada constitutes one of the last major biotic units in the continental United States to be colonized by the cowbird (reviewed in Gaines 1977, Rothstein et al. 1980). Colonization is still apparently in progress, as cowbirds are rare or absent from some wilderness regions and heavily forested areas (Verner and Ritter 1983). The recent arrival of cowbirds may be especially threatening to Sierran passerines. These populations have had no recent contact with parasitic birds, and thus their members may have relatively few or no adaptations to reduce the impact of cowbird parasitism. Furthermore, some Sierran passerines occur in small disjunct populations limited to patches of suitable habitat. Cowbird parasitism is especially likely to extirpate birds in such situations because there is no feedback between their abundance and that of the parasite. Parasite numbers may decline little if at all as the host declines, because most of the recruitment into the cowbird's population may come from more abundant, widespread host species. Passerines that seem to be endangered by cowbird parasitism in other regions have small, patchily distributed populations (Gaines 1974; Oberholser 1974; Post and Wiley 1976, 1977; Mayfield 1977, 1978; Pulich 1976). Evidence suggests that one favored host, the Warbling Vireo (*Vireo gilvus*), has already declined in Sierran areas where cowbirds are most common (Verner and Ritter 1983; see also Airola 1986). Therefore, it is important to develop techniques that can control cowbird populations if it is confirmed that Sierran passerines are undergoing serious declines due to cowbird parasitism.

Our earlier studies (Rothstein et al. 1980, 1984; Verner and Ritter 1983) suggested a feasible control technique. Throughout North America, cowbird distribution seems to be limited primarily by the availability of suitable foraging habitat, with the birds feeding mostly on the ground in areas of short grass, preferably in the immediate vicinity of grazing mammals (Friedmann 1929, Hamilton and Orians 1965, Mayfield 1965). Human development has created new foraging habitat as forests have been cut, arid land irrigated, and livestock introduced. Because it is largely undeveloped, however, the Sierra has relatively few such patches of "artificial" feeding habitat. Radio-tracking (Rothstein et al. 1984) demonstrated that Sierran cowbirds commute daily up to 7 km between widespread morning breeding ranges, where they are largely asocial in natural habitats; and localized artificial feeding sites (horse corrals, bird feeders,

etc.), where they are highly social in the afternoon. Thus, it may be possible to remove most cowbirds from an area within a radius of 7 km (154 km^2) or more by trapping birds at a single site for a short time. The effectiveness of such a removal program was tested in this study by removing cowbirds visiting a pack station over a one-month period in an area thought to contain little else in the way of artificial feeding habitat. In contrast to the trapout program currently used to remove cowbirds from the range of the Kirtland's Warbler (*Dendroica kirtlandii*) (Mayfield 1978, Kelly and De Capita 1982), our design relied on traps at one established feeding site, rather than on an extensive grid of traps designed specially for the trapping regime.

METHODS

The primary removal site was the Wishon Lakes Pack Station (WLPS), 1.2 km SSE of the Dinkey Creek Ranger Station, Sierra National Forest, Fresno County, California. Small numbers of cowbirds were also captured at the Camp El-O-Win horse corrals, 1.75 km southeast of WLPS. Both sites are at an elevation of 1710 m. Prior work (Verner and Ritter 1983 and Rothstein pers. obs.) showed that WLPS was the only feeding site within 15 km, an area covering 707 km^2, that attracted large numbers of cowbirds, often 40 or more at a time. To estimate the number of cowbirds visiting WLPS, we counted individuals present during 5-min periods spaced throughout the day (>0.5 h apart). Cowbirds were captured with "Potter" traps and, to a lesser extent, with a large (approx. 1.5 m^2) decoy trap baited with "wild bird seed." Yearling and adult males were differentiated by plumage (Selander and Giller 1960). Females were not aged.

To assess the area-wide effects of removing cowbirds from the 2 capture sites, birds were surveyed before and after the removal in 1981 at 38 points in all 15 meadows within 7 km of WLPS. We counted individuals of all bird species visually or aurally detected from a fixed point during a 10-min period between 05:30 and 09:30 PST. Meadows were chosen because cowbirds in this area are most common in these habitats and occur rarely in forests, the predominant local habitat (Verner and Ritter 1983). Because some survey sites within the same meadow were as little as 0.2 km apart, and hence well within the range of a single individual cowbird (Rothstein et al. 1984), each site did not constitute an independent datum. Rather, each meadow was treated as an independent datum, and analyses were done by analyzing the changes, between sampling periods, in total cowbird detections per meadow. We never detected cowbirds in 3 meadows, and these meadows are deleted from results reported here. The remaining 35 sites in 12 meadows ranged from 0.3 to 4.6 km from WLPS ($\bar{x}$ = 2.7, median = 2.6 km).

Observers surveyed each of the 35 sites during 3 periods: 7–13 July 1980, one year before the removal experiment (period A); 2–11 June 1981, immediately before cowbird removal at WLPS was initiated (period B); 29 June–8 July 1981, after the removal was nearly completed (period C). All 3 periods were within the early June to mid-July interval when Sierran cowbirds are at peak abundance (Rothstein et al. 1980). Although the peak of cowbird egg laying may vary from year to year and the use of afternoon feeding sites may vary within one season (Verner and Ritter 1980), we have found no variation in numbers of cowbirds occurring during the morning in breeding habitat from early June until mid-July when the birds leave the Sierra (Rothstein et al. 1980, Verner and Ritter 1983). To control for different

observers, only bird counts made by the same individual were compared. L.V.R. did counts at each site during all 3 periods; E.S. did counts only during periods B and C, the most critical ones for assessing effects of the removal. The 2 observers visited the same meadows on different days.

RESULTS

Cowbird occurrence at Wishon Lakes Pack Station.—We did frequent 5-min counts of cowbirds at WLPS during the time of day when cowbird numbers typically peak at pack stations (12:00–18:45). Observations began at 16:46 on 29 May, shortly before the first horses of the season arrived at 17:15. No cowbirds were detected that day despite nearly continuous observations from 16:46 until sunset; but cowbird numbers increased dramatically over the next 4 days (Fig. 1). The mean numbers of birds seen per 5-min count (Fig. 1) showed a significant rise between 29 May and 2 June (Kendall rank correlation tests: males, $\tau = 1.00$, $P = 0.008$; females, $\tau = 1.00$, $P = 0.008$), as did the peak numbers (Fig. 1) observed on each day (males, $\tau = 1.00$, $P = 0.008$; females, $\tau = 0.90$, $0.008 < P < 0.04$). Although it occurred in both sexes, the increase was much greater in males. This strong differential between the sexes is typical of Sierran pack stations and is especially pronounced at WLPS (Rothstein et al. 1980, Verner and Ritter 1983).

After a rapid increase, cowbird numbers became relatively stable by 2 June. The relation between time of day and cowbird numbers on 1 June (Fig. 2), the day on which we did the most 5-min counts, was typical of the diurnal pattern in cowbird numbers at Sierran feeding sites as shown by previous analyses in which data from many days were lumped (Rothstein et al. 1980; Verner and Ritter 1983). After numbers stabilized, they remained consistently above those seen shortly after the horses arrived (compare 29–31 May with 3–11 June) (Fig. 1).

The removal phase and trapping data.—The removal at WLPS began on 12 June, although 6 birds were captured on 8 June to provide decoys for our traps and for other cowbird studies. Traps were kept open and baited for 6–7 h on 8 of the next 9 days and sporadically thereafter (Fig. 3). Nearly all birds were captured in Potter traps. To determine if trapping had a detectable effect on numbers of cowbirds visiting the site, frequent 5-min counts were begun on 22 June. By 22 June, 102 (81.6%) of the 125 cowbirds ultimately caught at WLPS had already been removed (Fig. 3). The 5-min counts demonstrated significant decreases in cowbird numbers (*P*s with Mann-Whitney *U*-tests were each <0.001 for both males and females for numbers recorded during 3–11 June vs 22 June–1 July; data in Fig. 1). For example, male and female numbers, before the removal, peaked at 51 and 9, respectively, whereas the comparable numbers were

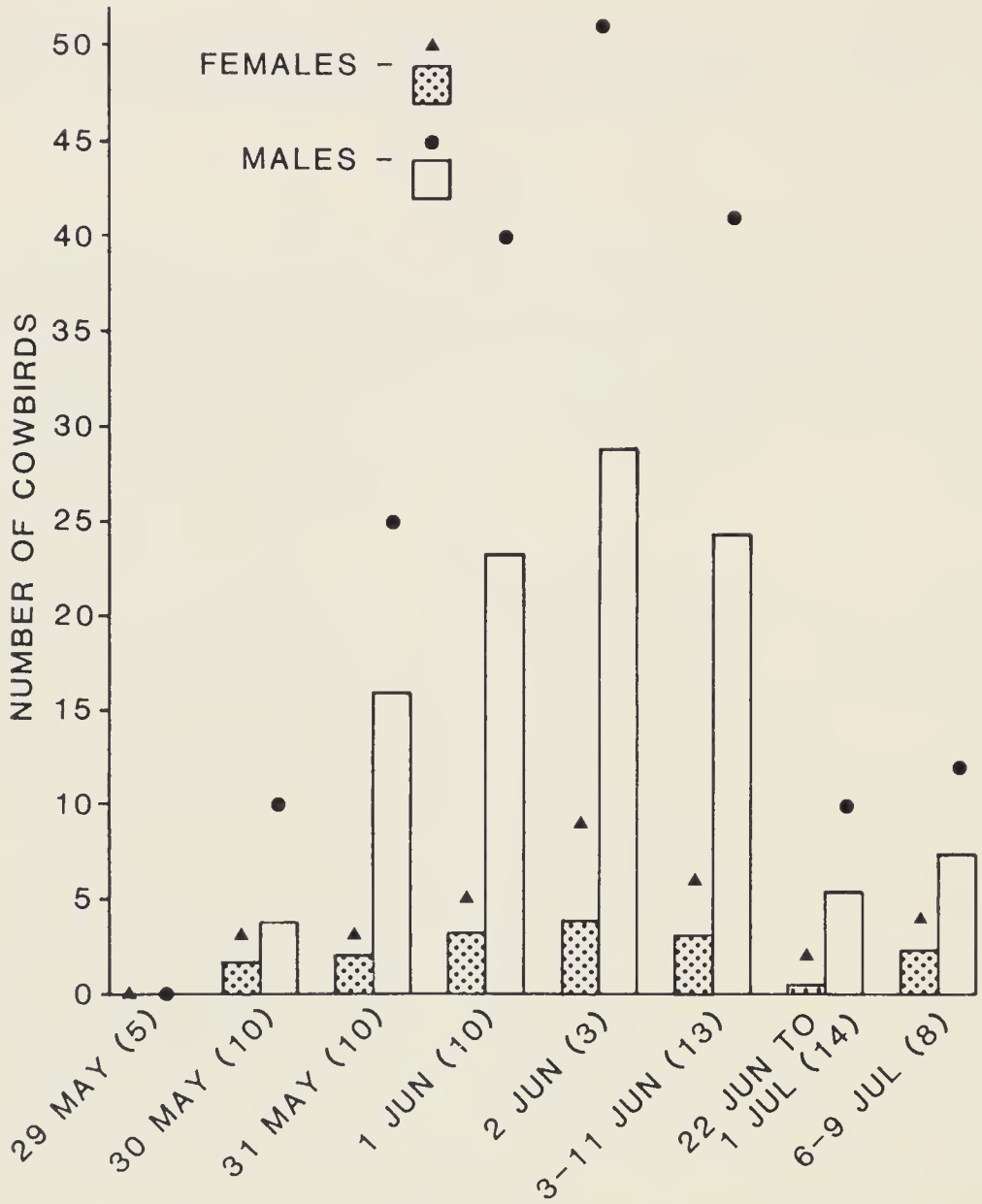

FIG. 1. Numbers of cowbirds recorded during 5-min counts at Wishon Lakes Pack Station during the daily period of peak abundance (12:00–18:45) on various dates. Bars represent mean numbers for the indicated dates; points (males) and triangles (females) indicate maximum counts. Sample sizes are given in parentheses after dates (i.e., number of 5-min counts taken ≥0.5 h apart). Horses were first brought to the pack station on 29 May. Peak counts of cowbirds stabilized by 2 June. Cowbird removal began on 12 June and was mostly completed by 22 June.

10 and 2 for the 22 June–1 July post-removal period (Fig. 1). However, cowbird numbers increased slightly by 6–9 July (Fig. 1), as the numbers of males and females seen at WLPS then were significantly higher than during 22 June–1 July ($P \leq 0.05$ and $P < 0.01$, respectively). This increase probably reflects immigrants from nearby regions, as banding studies (R. C. Fleischer and S. I. Rothstein, unpubl. data) have shown that some

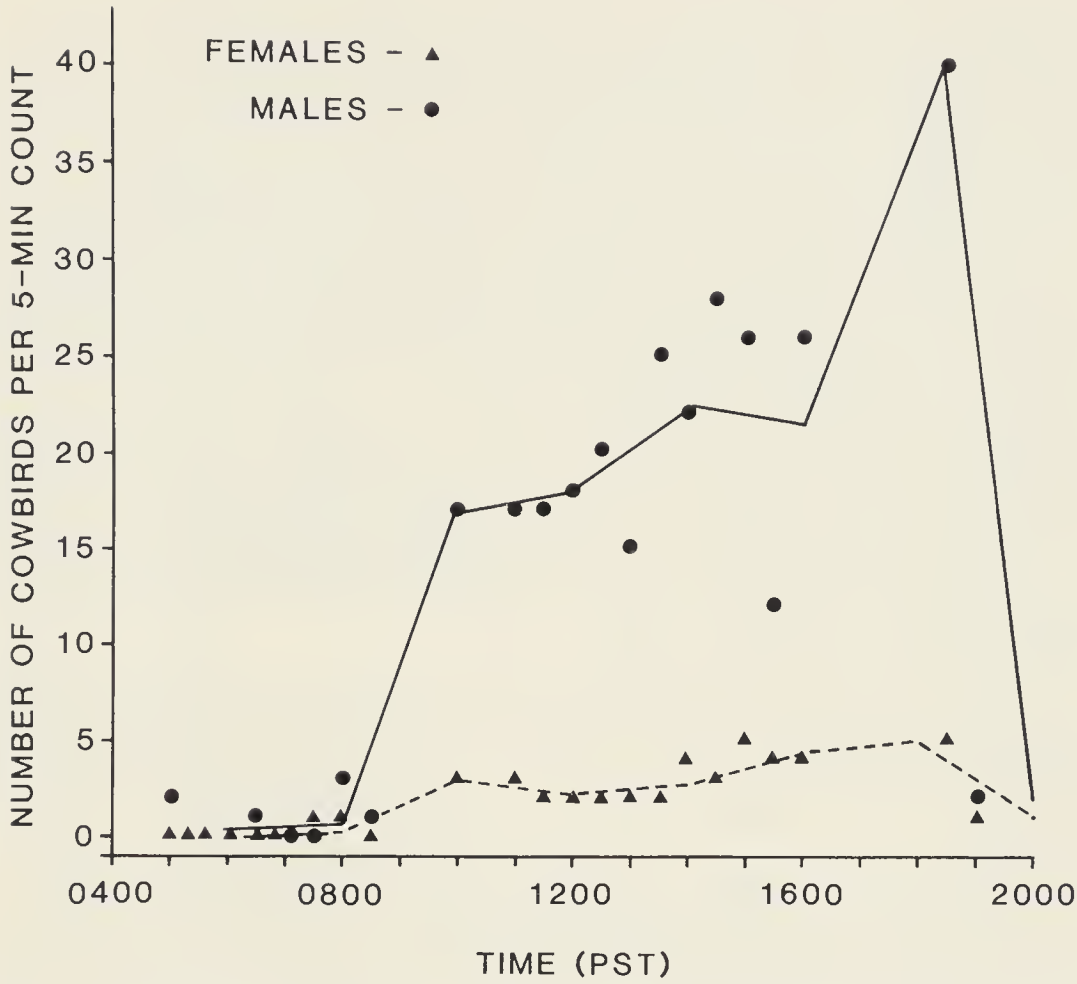

FIG. 2. Typical pattern of diurnal variation in cowbird numbers at Wishon Lakes Pack Station. The data are for 1 June when numbers began to stabilize. Solid and dashed lines represent 2-h means for males and females, respectively (05:01–07:00, 07:01–09:00, etc.).

Sierran cowbirds change their entire range during the breeding season and begin to use feeding sites 10 km or more from sites used earlier in the season.

The trapout data for WLPS showed 5 trends related to aspects of cowbird biology:

(1) The total number of birds caught, 96 males and 29 females, exceeded the largest numbers seen at one time, 51 males and 9 females.

(2) The sex ratio of captured birds differed from that of birds seen during counts. The former ratio was 3.3:1 (96M:29F); the latter was 5.7:1 (51:9) for the maximum numbers of each sex observed in one 5-min count and 7.6:1 (25.2:3.3) for the average number of each sex seen during the afternoon peak (12:00–18:45) in numbers between 2–11 June (Fig. 1).

(3) The numbers of captured adult and yearling males declined much more rapidly than did the numbers of females. Half of the trapping hours

at WLPS were on or before 19 June, not counting 2 days the traps were open for untimed intervals (8 and 25 June, Fig. 3). Half of 28 females, but 72.2% of 90 males caught during timed intervals, were caught on or before 19 June, a significant contrast ($\chi^2 = 4.77$, $P < 0.05$, for 14 of 28 vs 65 of 90). Similarly, the numbers of adult and yearling males captured per hour of trapping at WLPS (Fig. 3) declined significantly between 12 June and 7 July (Kendall rank correlation coefficients $\tau = -0.54$ for adults and $\tau = -0.55$ for yearlings, both Ps < 0.001). By contrast, the female capture rate showed no significant decline ($\tau = -0.05$, $P = 0.39$).

(4) Among males, yearlings were captured earlier in the removal process than adults. All 33 yearlings were caught on or before 23 June, whereas 9 of 63 adults were captured after that date (2-tailed Fisher's exact test, $P = 0.04$) (Fig. 3). Similarly, the proportion of each day's male captures that were adults was significantly correlated with the date of capture ($\tau = 0.45$, $P = 0.01$).

(5) Yearling males were caught earlier in the day: 11 of 17 males (64.7%) caught before 10:00 were yearlings but only 20 of 65 (30.8%) caught after 10:00 were yearlings ($\chi^2 = 5.2$, $0.02 < P < 0.05$, counting only captures on or before 23 June because no yearlings were caught after that date) (Fig. 3).

Trapping began at Camp El-O-Win on 26 June after horses were brought to that site. Fewer birds were captured there, 10 versus 125 at WLPS, possibly because trapping effort was less intense (Fig. 3). Also, the removal at WLPS had probably already resulted in a decline in area-wide cowbird numbers, and even under normal conditions El-O-Win attracted fewer birds than WLPS (unpubl. observations in 1980). The limited trapping data from El-O-Win support trends 2 and 4 (above) in the WLPS data and conflict with none of the others. The sex ratio for birds trapped at El-O-Win was unusually even (5M:5F) (Fig. 3), relative to the ratio for birds seen at Sierran feeding sites. Trapping at El-O-Win was late in the trapping period, and all the males captured were adults, as would be expected from the data for WLPS.

Eleven 5-min counts at WLPS from 14 June to 15 July 1983, averaged 5.0 males (range = 0–12) and 1.7 females (range = 0–3), with both distributions being significantly below the data for 2–11 June 1981 (Mann-Whitney U-tests, $P < 0.001$ for males and $P < 0.01$ for females) (Fig. 1). Data from 1984 also showed reduced numbers (M. D. Stafford pers. comm.), as did limited observations in 1982. We were unable to determine if this apparent long-range decline in cowbird numbers at WLPS was due to the 1981 trapout or to the fact that the proprietor of WLPS switched to a new horse food in 1982. This new food was "cubed hay" (densely

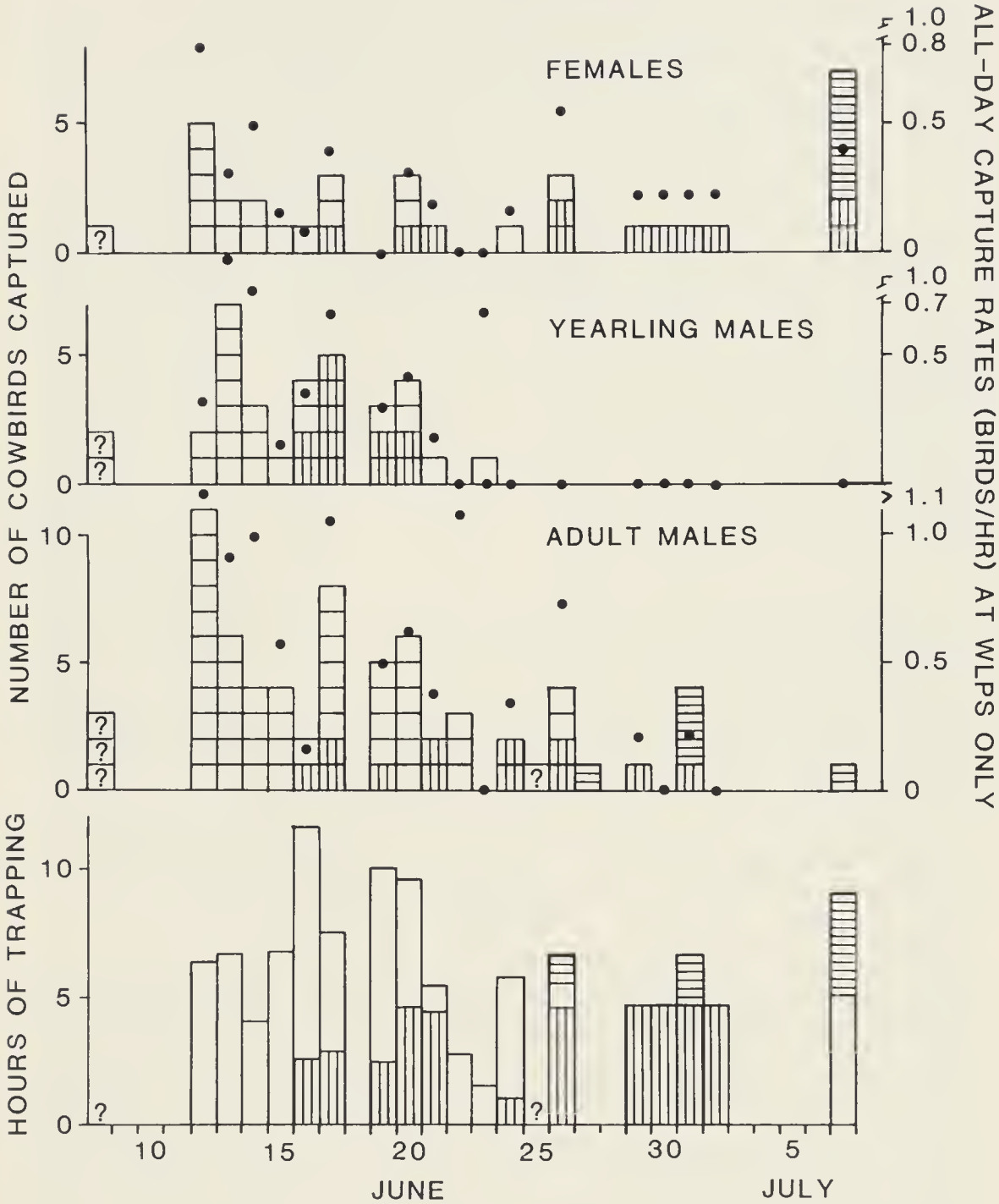

FIG. 3. Numbers of cowbirds captured and numbers of hours traps were kept open at 2 removal sites, Wishon Lakes Pack Station (vertical cross-hatching before 10:00, open blocks after 10:00) and Camp El-O-Win (horizontal cross-hatching). The hourly capture rates (solid dots) for each day of trapping at WLPS are also shown (except for 2 days, question marks, when times were not recorded).

TABLE 1

NUMBERS OF COWBIRDS DETECTED IN MEADOWS BEFORE (PERIODS A AND B) AND AFTER (PERIOD C) THE TRAPOUT PHASE AT WISHON LAKES PACK STATION

Meadow	No. observation sites[a]	Number of cowbirds (males : females) detected during sampling periods A to C				
		Ritter counts			Stevens counts	
		Period A (7–13 July 1980)	Period B (2–11 June 1981)	Period C (29 June–8 July 1981)	Period B (2–11 June 1981)	Period C (29 June–8 July 1981)
Cabin	4	6:0	5:0	2:0	5:0	8:1
Camp El-O-Win	1	0	0	0	1:0	0
Dinkey Crk. Dry	1	0	0	0	2:0	0
Dinkey Crk. Wet	1	0	0	1:0	1:0	0
Dinkey (Forbes)	5	1:1	8:1	2:0	6:3	2:0
Exchequer	2	0	0	0	2:0	0
Exchequer Heights	4	0	1:0	0	1:0	1:0
Glen	6	3:1	2:0	2:4	6:3	2:0
Lost	7	4:4	14:2	2:0	8:0	6:0
Pine Logging Camp	1	1:0	0	0	0	1:0
Pack Station	1	5:0	0	0	2:0	0
Flight Line 28 #221	2	6:0	3:0	0	4:3	2:0
Totals	35	26:6	33:3	9:4	38:9	22:1

[a] Number of points in each meadow at which 10-min counts were done. All points were surveyed once by each observer during each sampling period (except that Stevens did no counts during period A).

compressed hay cut into 3–4 cm cubes), and we suspect that it was less attractive to cowbirds than the regular hay used before 1982 because the birds probably couldn't easily separate seeds from the cubes.

Bird counts in the region surrounding the removal sites.—The sampling periods with the greatest potential of detecting an area-wide effect of the removal program are B and C, the periods immediately before and after the removal. Overall, Ritter listed 33 male and 3 female detections during period B, versus 9 and 4 during C (Table 1). This suggests a significant decline in males, as male detections were not divided equally between periods B and C (Binomial test, $P < 0.001$). A more conservative comparison using a Wilcoxon test (Siegel 1956, Rohlf and Sokal 1969) applied to the numbers of male cowbird detections per meadow showed a significant decline between periods B and C ($0.03 < P < 0.05$, $t = 1.5$, N = 6 meadows with changes in numbers of male detections). The data for females were too few for meaningful analyses.

Overall, Stevens had 38 male and 9 female detections during period B and 22 and 1 during C. Neither male nor female detections were divided equally between periods B and C (for males, $P = 0.026$; for females, $P = 0.01$). The number of male cowbird detections per meadow declined

significantly between periods B and C ($P = 0.03$, $T = 11$, N = 11). Female detections per meadow also declined, but the sample sizes were too small to show a significant result.

Another comparison of interest is that between the postremoval period in 1981 (period C) and a comparable time period in 1980 (period A) (Table 1). This comparison has the potential of indicating an area-wide effect of the removal, assuming that preremoval (period B) cowbird numbers in 1981 were not significantly below the 1980 (period A) counts. This assumption is reasonable because no significant or even strong trends emerged when periods A and B were compared. There were 26 male and 6 female detections during period A and 9 and 4, respectively, during period C. Male detections were not evenly divided between periods A and C ($P < 0.005$) but the female detections showed no trend (6:4). On a per meadow basis, male detections declined significantly between periods A and C ($P = 0.04$, $t = 5$, N = 8). Female detections were again too few for analysis.

A synthesis of these various tests indicates that the removal program depressed male abundance over a large area. All 3 comparisons (A vs C and B vs C for Ritter plus B vs C for Stevens) (Table 1) showed significant declines in both total male detections and male detections per meadow. Overall, Ritter detected only 27% (9/33) as many males after the removal as before, and Stevens detected only 58% (22/38) as many, giving a mean of 42.5% for these 2 samples. We found little clear evidence for a decline in female abundance, but most analyses suggested a slight decline.

DISCUSSION

Cowbird responses to horses.—The date on which horses are first brought to WLPS and other Sierran pack stations for the summer season varies by as much as 2 weeks (Verner and Ritter 1983), so the sudden rise in cowbird numbers after the horses arrived (Fig. 1) is unlikely to have been due to cowbirds accurately timing their migration into the Sierra Nevada to coincide with the appearance of horses. Also, 10-min counts in meadows during mid-May, before the horses arrived in 1981 (unpubl. data), indicated that there were nearly as many cowbirds present then as there were later in the season (period B) (Table 1). Thus the rapid increase in cowbird numbers at WLPS indicates that cowbirds were in the general area before the horses were present and that they frequently checked WLPS to assess its suitability for foraging. Although cowbirds were present in the area before horses arrived, the onset of peak egg-laying rates coincided closely with the arrival of horses and other livestock, thereby suggesting that the birds depend on these unnatural foraging associates for sustained breeding (Verner and Ritter 1983).

By monitoring cowbird numbers immediately after horses arrived at WLPS, we found that cowbirds were attracted to horse corrals by the presence of horses per se, not by the artificial habitat of corrals, i.e., bare dirt with hay and horse manure. Horses may increase the foraging value of pack stations because they and their fresh manure attract flies and other insects, their manure may have parasites, and pack station operators put out grain and fresh hay only when horses are present (although old manure and hay are usually abundant before horses arrive). Also, we found numerous insect larvae under hard caked manure and dirt at WLPS before the horses arrived, but the birds were unable to secure these until the horses walked over the area and broke up the soil.

The differing trapping patterns of adult and yearling males and of females.—That we were able to catch so many cowbirds and reduce the population size so effectively at WLPS, suggests that birds congregated there primarily for foraging rather than to engage in social behavior. This view agrees with our finding that the birds did not congregate at WLPS until horses were present. Although courtship and agonistic behavior are common at pack stations in the Sierra, and cowbirds often seem to be participating in a lek-like situation, we suggest that this social behavior is primarily or solely an outcome of the birds congregating to feed at a prime spot, not an inducement for the gregariousness itself. Significantly, the female capture rate (Fig. 3) did not decline towards the end of the removal phase despite the fact that male numbers at WLPS were greatly reduced. Had females visited WLPS to assess males in a lek-like situation, their visitation rates should have declined as male numbers went down.

It does not seem that a critical number of birds must be present for continued use of a feeding site. Thus cowbirds will apparently continue to feed at a site and become trapped even after their numbers begin to decline. However, radio-tracking studies conducted simultaneously with the removal experiment suggested that the birds visiting WLPS at any one time were a biased subsample of the local population. Some female cowbirds in this area often spent the afternoon in meadows, foraging among cattle (Verner 1983) and usually accompanied by 1 or 2 males. Thus the sex ratio in meadows was much closer to being even than it was at WLPS, and many cowbirds, especially females, in the area around WLPS did not show a consistent commuting pattern between disjunct morning and afternoon ranges. By contrast, all birds commuted to social feeding sites nearly every day in the eastern Sierra near Mammoth Lakes, where there is no network of mesic meadows used by range cattle (Rothstein et al. 1984). Although some or perhaps all local females visited WLPS on occasional days, trapping at WLPS was not a highly efficient way to reduce the local breeding population because it is more critical to

remove females than the more numerous males (sex ratios reviewed in Rothstein et al. 1986), yet the former made less use of WLPS.

The various trends in the trapout data support the view that the birds visiting WLPS at any one time were a biased subsample of the local population. A segment of the local population that did not visit WLPS every day accounts for the fact that the total numbers of both males and females caught greatly exceeded the highest numbers of each ever seen at one time. This discrepancy between numbers of birds observed and trapped at WLPS is probably also due to cowbirds sometimes perching high in trees surrounding the pack station and being less observable during our 5-min counts. The more even sex ratio among trapped birds than among birds seen at WLPS probably occurred because females, more than males, often failed to commute to WLPS every day. As the length of the trapout phase increased, more of these irregular visitors to WLPS were presumably added to the sample of trapped birds. This also explains the third trend in the trapout data, which showed that the capture rates for males declined over time whereas those for females did not. This latter result indicates that the relatively even sex ratio among trapped birds was not due solely to females being more likely to enter traps, as has been found for wintering cowbirds (Johnson et al. 1980).

The female capture rate at WLPS declined initially ($\tau = -0.47$, $P = 0.017$ for 12–24 June), although the overall rate showed no significant decline (Fig. 3). We suggest that this initial decline occurred because females with breeding ranges near WLPS visited it frequently, perhaps daily, and hence were rapidly trapped out.

Because yearling males were caught earlier in the trapout period and earlier in the day than adult males, we conclude that they spent more time at WLPS. Yearling cowbirds in California are much less successful at securing mates than are adults (Payne 1973, Rothstein et al. 1986, Yokel 1986), although the 2 age classes have similar success rates in the East (Darley 1968, Dufty 1982a). Thus among males, individuals that engaged in little or no breeding probably made greater use of WLPS than did more successful breeders. Although they do not maintain mutually exclusive territories (Dufty 1982a, b), male cowbirds interact agonistically (Rothstein et al. 1986, in press), perhaps in competition for local dominance. Yearling males are subordinate to adult males in the Sierra (D. A. Yokel pers. comm.), and some may be so effectively dominated in breeding habitat that they pursue a default strategy by investing less effort in mate procurement than do adults and by spending more time at prime feeding sites. That the ages of males at WLPS were skewed towards yearlings, which rarely mate (Rothstein et al.1986), is further evidence that females visited WLPS to feed rather than to assess potential mates.

Efficacy of the removal experiment, and management implications.— The mean number of male cowbirds seen per 5-min count during the afternoon at WLPS after the removal was only 23.0% of the mean before the removal (5.6 for 22 June–1 July vs 24.3 for 3–11 June; data in Fig. 1). The comparable figure for females was 12.5% (0.4 vs 3.2). These changes in numbers of cowbirds were much greater than those that occurred at WLPS during the 1980 breeding season (Verner and Ritter 1983), when no removals occurred. Thus, we conclude that the removal experiment brought about large and statistically significant declines in both males and females feeding at WLPS during the afternoon. However, the removal at WLPS apparently caused only moderate declines in the numbers of cowbirds occurring in the morning in breeding habitat in the area surrounding WLPS, and this decline was demonstrable only for males (Table 1). These results are in accord with the discovery that many females and some males did not commute to WLPS on a daily basis and with the various trends in the trapout data. Thus in the WLPS region, removal at 1 or 2 heavily used feeding sites over the one-month period we employed is not an efficient means of controlling cowbird numbers over a large area because of the availability of dispersed feeding habitat in the form of meadows with grazing cattle.

Because the female capture rate did not decline over our one-month trapout period, it is probable that we caught only a small fraction of the local female population. Thus future trapout programs should be continued for a longer period, because the lack of a significant decline in capture rate indicates that more and more females could have been caught at WLPS as they made occasional visits to the site. Another improvement would be to continue the trapout program for several years, as this too would result in the capture of an increasing proportion of the local females. Lastly, removal activity in meadows might also be an effective improvement to our trapout program. Such removal could be achieved by use of traps, but we suspect that simply shooting the small numbers of cowbirds present in each meadow would be more efficient. Both male and female cowbirds are attracted to playback of the female's chatter call if they are alone or in small groups of five or fewer (Dufty 1982b; Rothstein et al., in press), thereby making it easy to shoot cowbirds.

Unless they incorporate some of the improvements mentioned above, short-term removal programs such as the one we tested are likely to have only limited success in much of the Sierra Nevada because free-ranging cattle occur throughout most of the mountain range. Known major exceptions are the national parks (Yosemite, Sequoia, and Kings Canyon), where cattle grazing is not allowed, and some east slope areas such as the Mammoth Lakes region, where most of the local meadows are apparently

too dry to provide sufficient forage for cattle. Thus the removal technique tested in this study might be more effective in those parts of the Sierra, and in others where there are isolated pack stations or other forms of human development but no free-ranging cattle. However, even in the national parks and in the Mammoth area, cowbirds make use of alternative unnatural feeding sites, such as bird feeders and campgrounds (Rothstein et al. 1980), and the high availability of such sites in heavily visited national parks may offset the lack of cattle. Short-term removals are likely to be most successful in remote, high-altitude areas that are not reached by range cattle until cowbird breeding is over in mid-July (Rothstein et al. 1980, Verner and Ritter 1983) and that contain only one or several foci of human development such as pack stations or campgrounds.

Besides continuing the trapout phase for a longer period, we recommend that future programs continue to remove males, even though the number of females is obviously the most critical factor reducing host reproductive success. As indicated here, removal of males did not seem to make WLPS less attractive for females, and reduction of male numbers means that more traps are open and available for female captures.

Our most important finding relevant to cowbird control is that although Sierran cowbirds are most conspicuous while feeding during the afternoon in large groups at pack stations, they are adept at finding other sources of food due to human development. Furthermore, the birds in some large, conspicuous feeding groups may account for a disproportionately small share of the local breeding. Thus any plan to control cowbirds by trapping at a pack station must also consider all other forms of human activity in the area under consideration. Also, we repeat the suggestion made previously (Verner and Ritter 1983) that the impact of cowbirds can be managed by placing new foci of human activity (pack stations, campgrounds, etc.) in the Sierra Nevada and other semiwilderness regions near existing sites of human influence. Such a strategy will not open new areas to cowbird parasitism. The commuting distances over which cowbirds travel between breeding and feeding sites (Rothstein et al. 1984) can be used as a guide for siting new facilities.

We detected so few females in breeding habitat before the trapout procedure that there was little potential to find a significant decline in their numbers. Female detections were few, relative to male detections, because females are outnumbered by males (Rothstein et al. 1986) and are harder to detect in breeding habitat (Dufty 1981). Playing female chatter calls for a fixed time interval, instead of only counting birds under natural conditions (as in the present study), should be a more effective way to quantify cowbird numbers. However, repeated use of playbacks to detect cowbirds must incorporate suitable controls for habituation.

Dufty (1981) found that males were less likely to approach chatter playback if they had been exposed to playback on a previous day. Females showed no such change in responsiveness, and our playback experiments (Rothstein et al., in press) also indicate that female responses to chatter playback decline more slowly than male responses.

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CHANGE IN EDITOR

Dr. Charles R. Blem will serve as Editor of *The Wilson Bulletin* beginning with Volume 100. All manuscripts submitted for publication in the *Bulletin* should be sent to him at the Department of Biology, 816 Park Avenue, Virginia Commonwealth University, Richmond, Virginia 23284. All manuscripts received prior to 1 May 1987 will continue to be processed by Keith L. Bildstein.

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HOST-PARASITE INTERACTIONS OF BROWN-HEADED COWBIRDS AND DARK-EYED JUNCOS IN VIRGINIA

LICIA WOLF[1]

ABSTRACT.—In the Allegheny mountains of Virginia, 39% of Dark-eyed Junco (*Junco hyemalis*) nests contained at least one Brown-headed Cowbird (*Molothrus ater*) egg. Cowbirds laid an average of 1.7 eggs in each nest, and they removed an average of 1.2 junco eggs/nest. Removals primarily accounted for the reduction in mean number of junco young that were hatched and fledged in parasitized compared to nonparasitized broods. The majority of cowbird eggs were laid during the juncos' laying period, although some were laid slightly before or after the juncos' laying period. Most junco nestlings in nests with one cowbird nestling grew nearly as well as did those without cowbirds. Nest predation during incubation was higher in parasitized nests only in one of two years. Junco nests in relatively open areas appeared to have been more conspicuous both to cowbirds and predators. Brown-headed Cowbirds are recent invaders in this area, and possible antiparasite adaptations are discussed. *Received 7 Nov. 1985, accepted 12 Jan. 1987.*

Brown-headed Cowbirds (*Molothrus ater*) are opportunistic parasites that lay their eggs in the nests of many species (Southern 1958, Mayfield 1965, Friedmann et al. 1977). Some hosts (e.g., *Empidonax* spp. [Walkinshaw 1961], *Sayornis phoebe* [Rothstein 1975a]) suffer extreme reduction in reproductive success when one or more cowbird nestlings are present in the nest. Other species (e.g., *Melospiza melodia* [Nice 1937], *Seiurus aurocapillus* [Hann 1937]) are able to raise most of their own young in the nest along with cowbird young. The degree to which host nestmates can or cannot survive appears to be affected by the relative lengths of incubation of the cowbird and its host (Hann 1937, Payne 1977).

Host species often suffer clutch reduction due to the removal of and damage to eggs by cowbird females (Hann 1941, Carey 1986). In addition, cowbird nestlings have higher growth rates and attain a larger final size than the nestlings of many hosts (Hann 1937, Nolan 1978, Wiley 1986).

This study reports Brown-headed Cowbird parasitism of the Dark-eyed Junco (*Junco hyemalis carolinensis*) in the Allegheny Mountains of Virginia. Juncos are primarily ground-nesting and usually build their nests in road cuts or creek banks, often in edge habitats. Junco eggs in Virginia normally hatch after 12–13 days of incubation (Hostetter 1961, pers. obs.) vs 11 days for the cowbird. Juncos are able to raise some of their own

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nestlings with cowbird nestlings (White 1973). Because cowbirds have been present in this area only for about 20 years (D. W. Johnston, pers. comm.), the interactions of these species are of special interest in view of host-parasite coevolution.

STUDY AREA AND METHODS

The study was conducted within a 3.5-km radius of Mountain Lake Biological Station (MLBS), Giles County, Virginia, elevation 1198 m, between 17 May and 5 August 1983, and 9 May and 15 August 1984. The predominant habitat is deciduous forest, with oak (*Quercus* spp.), maple (*Acer* spp.), and hemlock (*Tsuga* spp.), interspersed with small fields and human settlements.

Junco nests were found during all stages of the nesting cycle and thereafter visited daily between 12:00 and 18:00 h. Junco and cowbird nestlings were weighed with a 10-g or 50-g Pesola spring scale to the nearest 0.1 g. Nestlings were not weighed after they reached eight days of age to prevent premature fledging. Some young were also weighed upon fledging.

Cowbird parasitism rates were calculated by determining the percent of active junco nests in which at least one cowbird egg was laid; active nests are those that were known to have been attended by a junco female the day before the junco would have, or had, laid her first egg. Because cowbird females occasionally remove cowbird eggs from nests (Nolan 1978: 377), nests that I found after the onset of junco laying may be subject to a bias of fewer cowbird eggs per nest (Rothstein 1975b). I was less attendant to individual cowbird eggs in 1983 than I was in 1984. In 1984 all eggs were marked on the day of laying, and individual eggs were closely monitored. I therefore included only the data from 1984 in the analysis of the number of cowbird eggs removed from junco nests.

Although I did not directly observe more than one cowbird parasitizing the same junco nest, I was fairly certain it occurred when two or more cowbird eggs appeared in a nest in one day, or when cowbird eggs in a nest were extremely different in size (cf. Friedmann 1929, Nice 1937:156, Hoy and Ottow 1964, McGeen and McGeen 1968, Dufty 1983).

In nests for which I did not know the exact date a cowbird egg was laid (e.g., if the nest was found after clutch completion), I estimated the approximate date of laying by backdating from the hatching date (assuming an eleven-day incubation period). If the nest failed prior to hatching, I estimated the date the cowbird egg was laid by assuming that it was laid within the first 3 days of the junco's 3–4 day laying period.

I examined selection of host nests by cowbirds with respect to the conspicuousness of nests by dividing the study area into two major vegetation zones or "habitat types" that may have influenced the cowbirds' ability to locate and parasitize junco nests. The first, designated "closed canopy," was along a rarely traveled dirt road that followed a canyon stream through relatively dense secondary riparian deciduous forest. The other, designated "open canopy," included all remaining sites in the study area, none of which included dense forest. To determine whether nests in open habitats were more likely to be found by cowbirds, predators, or both, I compared parasitism and predation rates of nests in both habitat types using chi-square analyses. I assumed that a nest was lost to a predator when (1) all eggs disappeared between daily nest checks or (2) I found shell remnants around the nest site. Nests that were known to have failed due to human interference (e.g., desertion of a nest during road construction near the nest) were excluded from the analyses.

In 1984 I removed cowbird eggs from nests in order to standardize junco clutch sizes for a separate study. If nests were found before clutch completion, I removed the junco eggs each day during the laying period and substituted them with cowbird or supplementary junco eggs. The full junco clutch (3–4 eggs) was replaced at the onset of incubation. Most

of the manipulated clutches in 1984 contained at least one junco and one cowbird egg during the laying period. Nests that contained only cowbird eggs were excluded from the analysis of number of junco eggs removed. Because cowbird females were prevented from removing junco eggs in 1984, the analysis of junco clutch size (resulting from potential cowbird interference) includes only data from 1983.

In 1983 I removed cowbird eggs and hatchlings so that only a single cowbird nestling remained in junco nests. Nestling growth is reported only for 1983. This study was carried out simultaneously with a study involving parental care in the Dark-eyed Junco, in which males were removed from some nests and not from others. Consequently, some cowbird young were raised in broods cared for by single female juncos, while others were raised by two parents. I therefore examine growth of cowbird and junco nestlings in broods raised by one parent, two parents, and with pooled data from all nests.

Nestling growth analysis.—I obtained 9 age-specific weights of individual nestlings during the period from hatching (day 0) to day 7 and at fledging (day 10 to day 11 for cowbirds, and day 10 to day 12 for juncos). For juncos, weights were analyzed in two ways: (1) individual weights of nestlings were combined among broods; individual nestlings were the sample unit (for ANOVA on junco nestling growth), and (2) the mean weight for each brood was obtained by calculating the mean weight of nestmates at the same age; the brood was the sample unit (for *t*-tests between parasitized and nonparasitized broods). The former method satisfies the assumption of homogeneous variances between groups, whereas the latter method satisfies the assumption of independence of samples for parametric statistics (e.g., broodmates may be more similar to each other than to nestlings in other broods) (Sokal and Rohlf 1981). I performed ANOVA tests on junco nestling weight for ages day 6, 7, and fledging (day 11–12), in which 3 independent variables were considered: cowbird (presence or absence in nest), male junco (presence or absence), and hatching date.

RESULTS

Seasonal variation in parasitism.—Parasitism in junco nests was highest during May in both years (Fig. 1). Thirty-five percent of 72 nests were parasitized in 1983, and 42% of 103 nests were parasitized in 1984. Parasitism declined to about 17% in late June. In both years, about 92% of the parasitism had occurred by late June; by mid-July cowbird eggs ceased to appear in nests, and cowbird adults were seen and heard infrequently.

Number of cowbird eggs in junco nests.—The maximum number of cowbird eggs found in parasitized junco nests was 3 in 1983 ($\bar{x}$ = 1.4 eggs/nest) and 6 in 1984 ($\bar{x}$ = 1.9 eggs/nest) (Fig. 1). In 1984 most nests contained one cowbird egg, 2 eggs being the next most common. In 1983 one-cowbird-egg nests were relatively more common than in 1984. The frequency distribution of cowbird eggs in junco nests was statistically similar between both years (2 by 4 contingency table, 2 years with 4 categories of egg frequencies; 1, 2, 3, and 4–6 eggs/nest, $\chi^2 = 5.1$, df = 3, $P > 0.15$). All clutches that received 3 or more cowbird eggs were laid in May; such nests appeared to contain eggs laid by more than one cowbird female (Fig. 1). I probably underestimated cowbird egg numbers because of the occasional removal of cowbird eggs by cowbirds, which may have gone undetected in 1983. Nests that contained one cowbird egg/nest were

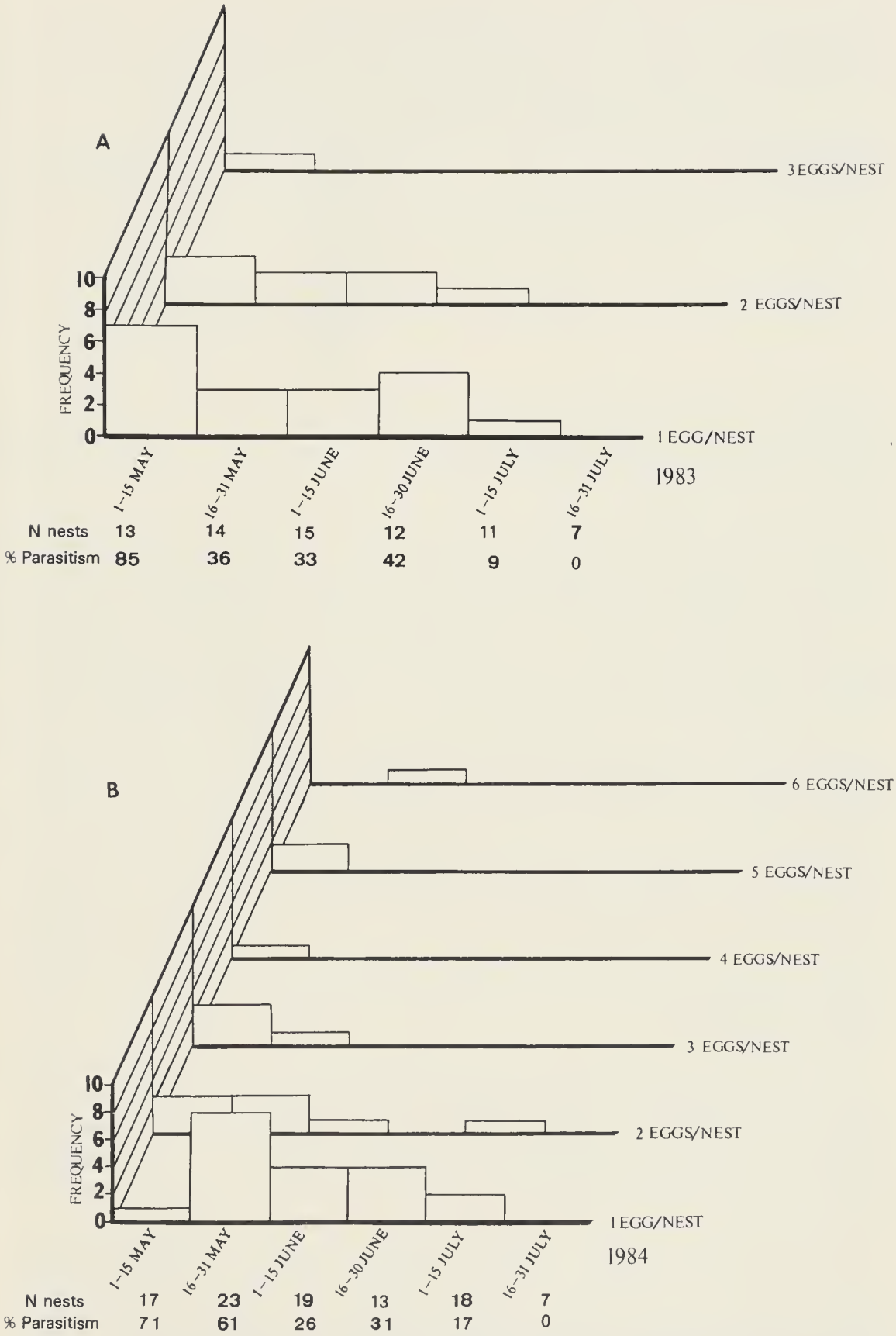

FIG. 1. Number of junco nests containing from one to six cowbird eggs/nest by 2-week increments in 1983 and 1984. Only nests in which the total number of cowbird eggs laid was known are included.

TABLE 1

POISSON DISTRIBUTIONS OF THE NUMBER OF COWBIRD EGGS LAID IN JUNCO NESTS OF ALL NESTS AND ONLY PARASITIZED NESTS, 1983 AND 1984 COMBINED[a]

Number of cowbird eggs/nest	Observed frequency[b]	Expected frequency of all nests	Expected frequency of parasitized nests
0	90	76.09	
1	37	54.63	12.07
2	20	19.61	20.51
3	5	4.70	17.43
4	1	0.84	9.89
5	2	0.12	4.20
6	1	0.01	1.43
N		156	66

[a] See text for statistics.

[b] Includes only clutches laid before 15 July.

less frequent than expected, and those that were not parasitized were more frequent than expected (combining categories of 4–6 eggs/nest, $\chi^2 = 17.6$, df = 3, $P < 0.001$) (Table 1). When the distribution of only parasitized nests is examined, however, nests containing one cowbird egg were more frequent than expected ($\chi^2 = 69.7$, df = 2, $P < 0.0001$) (Table 1).

In 1984 there were 9 instances in which I was able to document that cowbird eggs were removed from junco nests, presumably by other cowbirds (cf. Hann 1937, 1941), although I did not directly observe cowbirds removing eggs. In 7 of the 9 cases, a new cowbird egg was present at the time I discovered the disappearance of the old egg (or else it had appeared within 2 days), indicating that the nest had been visited by a cowbird. Usually only one egg disappeared a day, leaving the rest of the clutch intact; other evidence (i.e., eventual fledging of the brood) suggested that the egg removals were not due to predators. Removal of eggs by cowbirds is discussed below.

Parasitism in relation to habitat and predation.—In 1984 only, nests in the closed canopy site were parasitized significantly less often than those in the open canopy site (1983: open canopy, 41% parasitized, N = 44; closed canopy, 32% parasitized, N = 28, $\chi^2 = 0.56$, $P > 0.1$; 1984: open canopy, 45% parasitized, N = 73; closed canopy, 20% parasitized, N = 30, $\chi^2 = 7.67$, $P < 0.01$).

In 1983 no difference occurred between parasitized and nonparasitized clutches in the proportion of nests in which at least one egg of either species hatched. In 1984, however, significantly more parasitized nests than nonparasitized nests failed during incubation (55 vs 31%; $\chi^2 = 5.41$, $P < 0.05$).

Nest desertions.—Six nonparasitized and 11 parasitized nests were deserted, either because of human disturbance or other unknown factors. Four desertions in nonparasitized nests occurred before any eggs were laid in the nest. One female deserted after laying one egg. Desertions in parasitized nests occurred (1) when a cowbird egg had been laid in the nest before the junco laid (N = 3) or (2) when junco eggs were removed from nests (N = 4). The latter nests were always deserted before the second day of incubation. Two juncos deserted their nests before clutch completion after I replaced their eggs with cowbird eggs. The remaining 3 nests (one parasitized, two nonparasitized) were probably abandoned as a result of other human disturbance.

Removal of junco eggs by cowbirds.—As in other studies of cowbird parasitism in small hosts, cowbirds usually removed 1–2 eggs/nest (McGeen and McGeen 1968, Nolan 1978, Walkinshaw 1983). In 1983 the mean number of junco eggs removed from parasitized nests was 1.0 egg/nest (0 eggs removed = 42%, 1 egg removed = 20%, 2 eggs removed = 21%, 3 eggs removed = 11%, N = 19 nests). In 1984 the mean number of junco eggs removed from parasitized nests was 1.4 eggs/nest (0 eggs removed = 25%, 1 egg removed = 32%, 2 eggs removed = 32%, 3 eggs removed = 7%, 4 eggs removed = 4%, N = 28 nests). In 1983 nearly half of the nests had no junco eggs removed, but in 1984 nests with one and two eggs removed were more common. These figures may be influenced partially by my collection of junco eggs and replacement with cowbird eggs.

Timing of junco laying with respect to cowbird laying, egg removal, and final clutch size.—When 1983 and 1984 data are combined, 34% of the cowbird eggs (N = 14) were laid prior to the juncos' first egg, 46% (N = 19) were laid during the laying period, and 20% (N = 8) were laid during incubation.

Removal of eggs from nests by cowbirds apparently occurred throughout the day. One junco egg disappeared from one nest between 10:30 and 14:45 h, another between 10:15 and 11:05 h. A cowbird egg disappeared between 14:00 and 17:00 h.

Final junco clutch size of parasitized and nonparasitized nests was calculated only for 1983 nests. In 1983 the final clutch size of clutches completed before 15 July was significantly smaller for parasitized clutches than it was for nonparasitized clutches (parasitized: $\bar{x} = 3.0$, mode = 3, N = 13, nonparasitized: $\bar{x} = 3.3$, mode = 4, N = 22, median test; $\chi^2 = 8.33$, $P < 0.025$).

Hatching order.—As I removed all but one cowbird from each junco nest in 1983, the following includes broods with only one cowbird nestling. Of the 11 cowbird eggs present in 1983 nests in which I knew both the date of incubation onset and the hatching date, 9 cowbirds hatched the

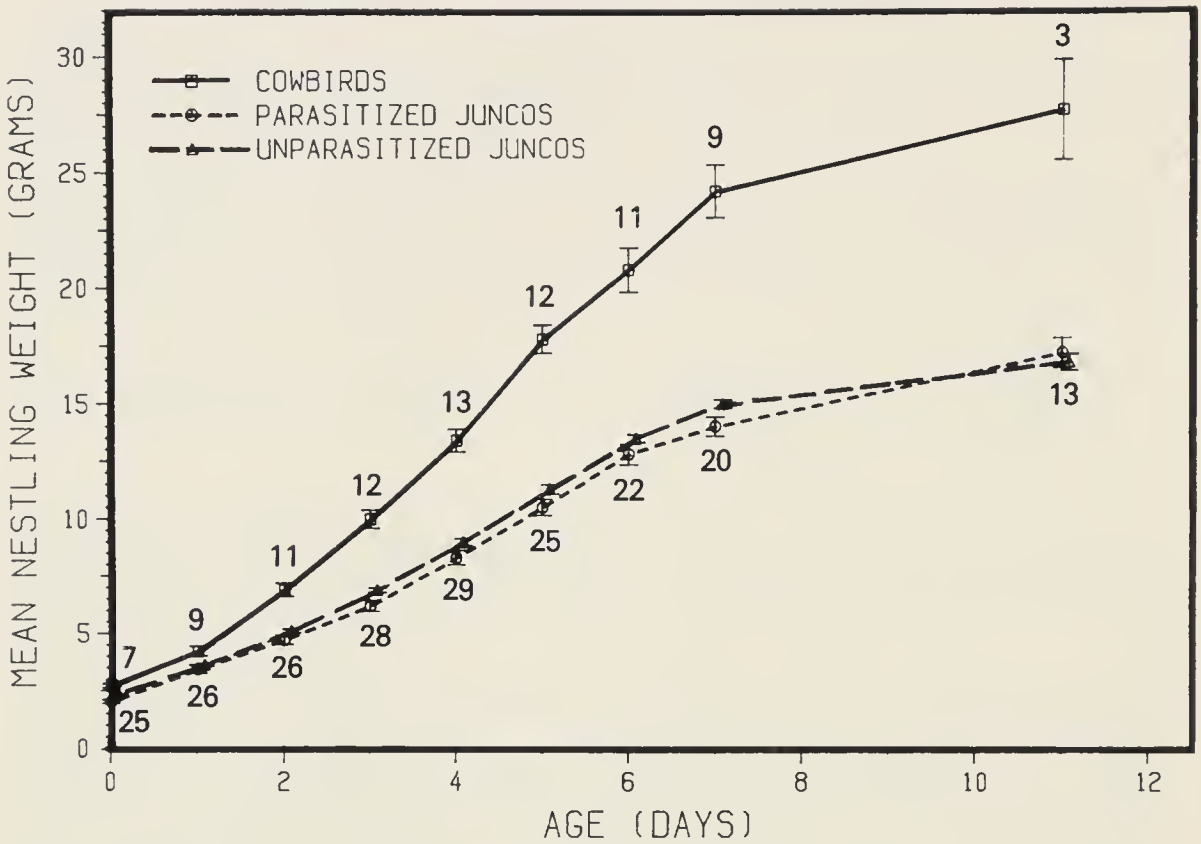

FIG. 2. Growth of cowbird nestlings and junco nestlings in nests with and without cowbirds in 1983. Cowbird weights represent individual nestlings; junco weights are comprised of the mean junco nestling weight in a brood for each age. The number of cowbird nestlings and parasitized junco broods at each age is shown above the cowbird curve. The number of nonparasitized junco broods at each age is shown below the junco curves. Vertical bars indicate ±1 SE.

day before their junco nestmates, one hatched the same day, and one hatched the day after the first junco nestling. Because of the predominance of earlier hatching by cowbird young, most cowbird nestlings were considerably larger than their junco nestmates (by about 1 g) by the time the juncos hatched (mean hatching-day weight was 2.7 g for cowbirds and 2.3 g for juncos) (Fig. 2). The presence of a single cowbird nestling apparently had no negative effect on junco growth (t-tests between weights of parasitized and nonparasitized juncos, $P > 0.05$).

Influences of parental care and hatching date on nestling growth.— Cowbird young fed by one junco parent were lighter than those fed by two parents, but the samples are too small for statistical analysis ($\bar{x}$ day-7 cowbird weight with one parent = 22.4 g, N = 4, $\bar{x}$ day-7 cowbird weight with two parents = 25.7, N = 5). Cowbirds in one-parent broods tended to be lighter than those in two-parent broods after day 4. When compared to parasitized juncos in broods with two parents, parasitized junco nest-

TABLE 2
MEAN NUMBER AND PERCENT OF JUNCO YOUNG THAT HATCHED AND FLEDGED IN PARASITIZED AND NONPARASITIZED NESTS[a]

	Number of young hatched	% eggs hatched	Number of young fledged	% hatchlings fledged
Parasitized nests	2.4 ± 0.87 (13)[b]	85	1.5 ± 1.1 (8)	75
Nonparasitized nests	3.3 ± 0.63 (26)[c]	94	2.7 ± 1.1 (12)	82

[a] Values were calculated from the number of eggs laid and numbers of young that were present at hatching and fledging.
[b] $\bar{x}$ ± SD (number of nests).
[c] One case omitted in which the single cowbird egg was removed before incubation by the investigator.

lings in broods without male care showed depressed growth from about day 3 to day 7. The weight difference ranged from 0.5 to 1.1 g, but these differences are not statistically significant ($P > 0.05$). Both cowbird and junco young of a given age tended to be relatively lighter early in the season (linear regressions with cowbird nestling weight on hatching date for young 3–7 days of age, $P < 0.05$). The correlation of weight with hatching date, however, may be influenced by the relatively greater number of early-season one-parent broods.

Analysis of variance of junco weights on days 6 and 7 showed that nonparasitized and later-season nestlings tended to be heavier (Day 6: overall $F = 7.4$, $P = 0.001$; Day 7: overall $F = 4.6$, $P = 0.002$). Hatching date was the main influence for both ages (partial $P < 0.05$). In addition, there were significant interactions between the variables cowbird and male (partial $P < 0.02$), and between hatching date and male (partial $P = 0.001$). These trends were not apparent at fledging. The analysis indicates that the absence of a male had a negative effect on junco nestling growth, but that this effect was confounded by the negative effect of a cowbird and the early hatching date of the young.

Survival of young.—The proportions of junco eggs that hatched and those that fledged (in broods in which at least one young fledged) were only slightly reduced in parasitized nests (Mann-Whitney U-test; $P > 0.1$) (Table 2). The absolute numbers, however, of junco young that hatched and fledged from parasitized nests were significantly reduced (one-tailed t-tests; young hatching, $t = 3.68$, df = 37, $P < 0.001$; young fledging, $t = 2.43$, df = 18, $P < 0.025$).

There was no difference during the nestling stage in the rate of complete nest predation between parasitized and nonparasitized broods (76% vs 64% of broods fledged, $\chi^2 = 0.66$, $P > 0.5$). Starvation occurred in only 2 nests in 1983; one was nonparasitized, and the other had 2 cowbirds (the only brood with 2 cowbirds). In another nest the cowbird apparently

crowded its 2 junco nestmates out of the nest over the course of 3 days. At this point the cowbird weighed more than twice as much as its junco nestmates.

The survivorship of the fledgling cowbirds could be determined adequately for only 6 families. In 2 of the broods the cowbird disappeared within 4 days after fledging, and in 4 broods it survived to independence (fledglings were considered independent after 15 days postfledging, when they were observed to feed themselves). Two of the surviving cowbird fledglings were the only fledglings remaining in their brood. The remaining two cowbird fledglings were raised in families with one and two junco fledglings, respectively.

DISCUSSION

Parasitism in relation to habitat and predation.—Overall parasitism and predation rates in this study were heavier in 1984 than in 1983; in 1984 parasitism and predation rates were greater in open habitats than in forested habitats. It seems possible that both cowbirds and predators may take advantage of the relative conspicuousness of nests in the more open areas. Yearly variation in the rate of parasitism in different habitats may result from fluctuations in either host availability or cowbird density (McGeen and McGeen 1968, Rothstein et al. 1984).

Nests of the Oregon race of the Dark-eyed Junco (*Junco hyemalis oreganus*) in the Sierra Nevada in California were parasitized almost exclusively in open meadow areas (White 1973). Similarly, parasitized Song Sparrow nests in Ohio tended to be less concealed than were nonparasitized nests (Nice 1937:162–163). Nest concealment apparently had no influence on cowbird parasitism in Song Sparrows breeding on Mandarte Island, British Columbia, (Smith 1981), or in Prairie Warblers (Nolan 1978:411).

Junco nests at MLBS contained cowbird eggs laid by one or two cowbirds, (as indicated by distinct types of cowbird eggs within a nest; Dufty 1983, Fleischer 1985). Radio-tracking studies have shown that although individual female cowbirds occupy home ranges that tend to be exclusive of other females (Dufty 1982, Rothstein et al. 1984), overlap in host nests does occur.

Cowbird reproductive success and the effect of cowbirds on junco reproductive success.—The reproductive success of Brown-headed Cowbirds, although lower than that of juncos, was evidently high compared with most cowbird populations studied (Scott and Ankney 1980); 57% survived during the nestling stage, and 67% of the fledglings survived to independence. This survivorship measure may have been increased because only a single cowbird nestling was present in any given junco nest. My removal of male juncos, however, may have confounded cowbird postfledging

survival. Cowbird mortality was apparently higher both in the Sierra Nevada (White 1973) and in British Columbia (Smith 1981). Woodward (1979) found that the highest mortality in cowbirds occurred during the first few days after fledging for several North American passerine hosts.

Fewer junco young hatched and fledged in parasitized than in nonparasitized nests, probably because of the removal of and damage to junco eggs by cowbirds (Friedmann 1929, Nice 1937:157, Hoy and Ottow 1964, Carey 1986). Once hatched, however, most junco nestlings raised with cowbirds appeared to fare as well as those in nonparasitized broods. Several interacting factors contributed to the variation in cowbird and junco nestling weight. In 1983 both cowbird and junco nestlings were heavier later in the season, and the presence of cowbirds combined with the absence of a male parent resulted in lower junco nestling weights. However, the fledging weight of juncos was not correlated with survival to independence (Wolf, Ketterson, and Nolan, unpubl. data). The mean number of independent junco young produced over the entire season by females hatching at least one parasitized brood was significantly less than for unparasitized females.

Possible antiparasite adaptations.—My findings suggest that cowbirds may be exerting a slight negative impact on the junco population in the Allegheny Mountains, even though the density of breeding juncos in this population appears to be similar to, if not higher than, the density found by Hostetter in 1936–1938 (1961) (5.0 nests/km then vs 12.4 nests/km now), well before cowbird invasion occurred (however, the higher number of nests in my study may be due to nests found in areas other than on the roads). Thus I consider below whether adaptations against brood parasitism may be incipient in this junco population (Rothstein 1975b).

Payne (1977) suggested 3 primary mechanisms that could reduce or avoid brood parasitism: (1) A shift in breeding season: The host breeds at a time during the season that circumvents that of the parasite. (Multiple-brooding is included in this category.) (2) Nest desertion or burial of eggs in the nest by building over. (3) Ejection of parasite eggs: This behavior is not known to occur in juncos and will not be considered further. A fourth possibility, vigilance toward the parasite at the nest site (Robertson and Norman 1976, Smith et al. 1984), was not assessed in this study, and I do not consider this possibility further.

Late-season broods may partly compensate for the decreased reproductive success suffered in early-season broods in Dark-eyed Juncos. As the probability of parasitism after mid-June decreases (Fig. 1), clutches initiated during this period are relatively cowbird-free. However, second and late clutches occurred even before cowbird invasion (Hostetter 1961), and thus cannot be considered a behavior selected for by parasitism.

In 1983 few females deserted their nests as a consequence of parasitism,

but desertions were more frequent in 1984 (i.e., when cowbirds had laid eggs or I had substituted cowbird eggs). Furthermore, most desertions occurred before the clutch was complete. These desertions may have been an evolved response to partial clutch reduction, caused either by cowbirds removing host eggs, or by predation (Wiley 1985, Rothstein 1986). Desertion of small clutches, especially early in the season, would allow the host to renest rapidly with a full clutch, thus maximizing its reproductive output.

Do Dark-eyed Juncos in southwest Virginia show antiparasite adaptations? Although some nest desertions of parsitized clutches did occur, alternate explanations (e.g., response to nest predation) are possible. As the reproductive success of juncos appeared to decrease as a result of brood parasitism, antiparasite adaptations would be expected to evolve (Rothstein 1975a). The apparent lack of antiparasitic behavior to date may be due to the fact that juncos have not been exposed to cowbird parasitism long enough for antiparasite adaptations to evolve. On the other hand, a high predation rate results in the destruction of most nests, and, perhaps, the combination of costs resulting from nest desertion or egg burial (in terms of breeding time and energy investment) and the small average impact of cowbirds on junco reproductive success exceeds the costs of avoiding parasitism. Thus, factors other than cowbird parasitism may have a greater influence on lifetime reproductive success (cf. Payne 1969, McGeen 1972, Smith 1981). In juncos and other species, high variability in parasitism pressure from year to year appears to be common (Mayfield 1960, Walkinshaw 1961, 1983, Nice 1937, McGeen 1972, Nolan 1978, Smith 1981). This variation may result in insufficient selective pressure for the evolution of antiparasite behavior. Experimental studies (cf. Rothstein 1975b, 1986) are needed to test whether antiparasite adaptations have indeed evolved in the Dark-eyed Junco.

ACKNOWLEDGMENTS

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NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANTS

The North American Bluebird Society announces the fifth annual grants in aid for ornithological research directed toward cavity nesting species of North America with emphasis on the genus *Sialia*. Presently three annual grants of single or multiple awards totaling $7,500.00 are awarded and include:

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Further guidelines and application materials are available upon request from Theodore W. Gutzke, Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746. Completed applications must be received by December 1, 1987; decisions will be announced by January 15, 1988.

NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANT AWARDS

The North American Bluebird Society is proud to announce the presentation of the fourth annual research grant awards. The 1987 recipients are as follows:

Bluebird Grant

Wayne H. Davis.—Eastern Bluebird and European Starling: Competition for Nest Sites. $1125

Steven G. Parren.—Bluebird Nest Box Selection by Competing Passerines. $950.

Student Grant

Danny J. Ingold.—Nesting Phenology and Competition for Nest Sites Among Red-headed and Red-bellied Woodpeckers and European Starlings in East Central Mississippi. $400

Kimberly A. With.—Effects of Brood Size on the Parental Care of Western Bluebird Nestlings. $836

General Grant

Vasiliki Demas.—Effect of Blowfly Parasitism on the Growth and Development of Western Bluebird Nestlings. $1000

Gregory Hayward.—Potential of Nest Boxes for Monitoring and Managing Boreal Owls. $1050

William McComb.—Microclimatic Characteristics of White-breasted Nuthatch Roost Sites. $1110

The North American Bluebird Society annually provides research grants in aid for ornithological research directed toward cavity nesting species of North America with an emphasis on the genus *Sialia*. Information and application materials are available from Theodore W. Gutzke, Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746.

Wilson Bull., 99(3), 1987, pp. 351–368

CROSSBILL FORAGING BEHAVIOR, BILL STRUCTURE, AND PATTERNS OF FOOD PROFITABILITY

Craig W. Benkman[1]

Abstract.—The rate at which White-winged Crossbills (*Loxia leucoptera*) and Red Crossbills (*L. curvirostra*) extract and consume seeds from conifer cones was measured in the laboratory. White-winged Crossbills were more efficient than Red Crossbills at handling small seeds, but the converse was found for large seeds. Time required to extract seeds (interseed interval) from conifer cones depended on the stage of cone ripeness and was usually greater than seed-husking time. Interseed intervals were greatest, and intake rates (mg kernel ingested/sec) lowest, when cones were closed or when they were open, but had shed most of their seed. White-winged Crossbills were more efficient than Red Crossbills when foraging on spruce (*Picea* spp.) cones and when cones were open and full of seeds. Red Crossbills were more efficient while foraging on pine (*Pinus* spp.) cones and when seeds were difficult to extract from between cone scales. The differences in foraging efficiency were related to morphological differences between the two species; White-winged Crossbills have more slender, shallower, and less powerful bills than do Red Crossbills. The differences in foraging efficiency are consistent with patterns of crossbill distribution and conifer use in the field. Differences in bill structure may be related to increasing foraging efficiency during periods of food limitation. Differences in foraging efficiency among individual crossbills were consistent with the hypothesis that variation between the efficiency of individuals should be less when birds forage on foods used during periods of greatest food limitation than when they forage on foods used during less stressful times. *Received 7 Nov. 1986, accepted 24 Feb. 1987.*

A common assumption in avian foraging ecology is that differences in bill structure cause differences in foraging efficiency. Most foraging studies recognize two components of foraging behavior: search time and handling time (Pyke et al. 1977). For seed-eating birds, handling time is often assumed a constant for a given seed type (e.g., Pulliam 1980), whereas search time varies as a function of prey density. Among birds that feed on conifer seeds, time spent searching for conifer cones may contribute little to overall foraging time, and time spent husking a given seed type can be assumed constant. Time spent removing seeds from cones, however, may be the most variable and time consuming component of foraging. Furthermore, time spent removing seeds from cones may require more specific adaptation than that required to husk seeds. The correlation observed between the bill size of different species of crossbills (*Loxia* spp.) and the size of cones used (Griscom 1937; Lack 1944a, b, 1947; Southern

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TABLE 1
BILL AND BODY MEASUREMENTS OF WHITE-WINGED AND RED CROSSBILLS USED IN THE EXPERIMENTS

	White-winged Crossbill	Red Crossbill	Ratio of WWC to RC
Bill depth (mm)	8.1 ± 0.1[a]	9.6 ± 0.3	1:1.18
length (mm)	15.1 ± 0.7	16.6 ± 0.4	1:1.10
width (mm)	7.7 ± 0.4	10.4 ± 0.2	1:1.35
Wing length (mm)[b]	88.0	95.5	1:1.09
Body mass (g)[c]	26.4 ± 1.3	35.9 ± 1.7	1:1.36
Body mass$^{1/3}$	2.98	3.30	1:1.11

[a] $\bar{x}$ ± SD.
[b] Based on measurements (middle of range) in Griscom (1937).
[c] Weight at time of capture. White-winged Crossbills were caught in August; Red Crossbills were caught in late March and in early April. Winter weights are known to be higher than summer weights for cardueline finches (Newton 1972). Thus, the relative differences in mass probably are not as great as shown here.

1945) indicates that the procurement of seeds from cones has required specific adaptation.

In northeastern North America, White-winged Crossbills (*L. leucoptera*) most frequently forage on white spruce (*Picea glauca*), black spruce (*P. mariana*), and tamarack (*Larix laricina*); whereas Red Crossbills (*L. curvirostra*) most often forage on pines (*Pinus*), particularly white pine (*P. strobus*) (Benkman, in press). In the laboratory, I measured the efficiencies of both White-winged and Red crossbills foraging on the cones of seven species of conifers. Analyses of both intra- and interspecific differences in foraging efficiency were employed to interpret differences in bill structure and conifer use in the field, and to test the hypothesis that selection for bill structure has been strongest during periods of greatest food limitation. I describe the foraging behavior of crossbills to facilitate interpretation of the comparative foraging data. Elsewhere (Benkman, in press), I use foraging data gathered in the field to demonstrate that food profitability (mg kernel ingested/sec) influences crossbill diets, movements, and abundance.

METHODS

Three White-winged Crossbills (*L. l. leucoptera*) were captured in Laurentides Reserve, Quebec, in August 1984. Eight Red Crossbills were captured in Albany, New York, in April 1982 (Table 1, Fig. 1). The Red Crossbills studied in the laboratory represent the subspecies *L. c. bendirei* (based on body mass, wing chord, and bill depth, width, and length measurements; pers. obs., Dickerman 1986). When captured, all birds were in adult plumage, and at the time of the experiments, all birds were "after-hatching-year" birds.

Captive crossbills were housed in a 4 × 3 × 2.5 m indoor aviary that was partitioned with hardware cloth (1.2 cm mesh) into two sections. White-winged Crossbills were housed in one of the sections, which was approximately one half the volume of the adjacent section

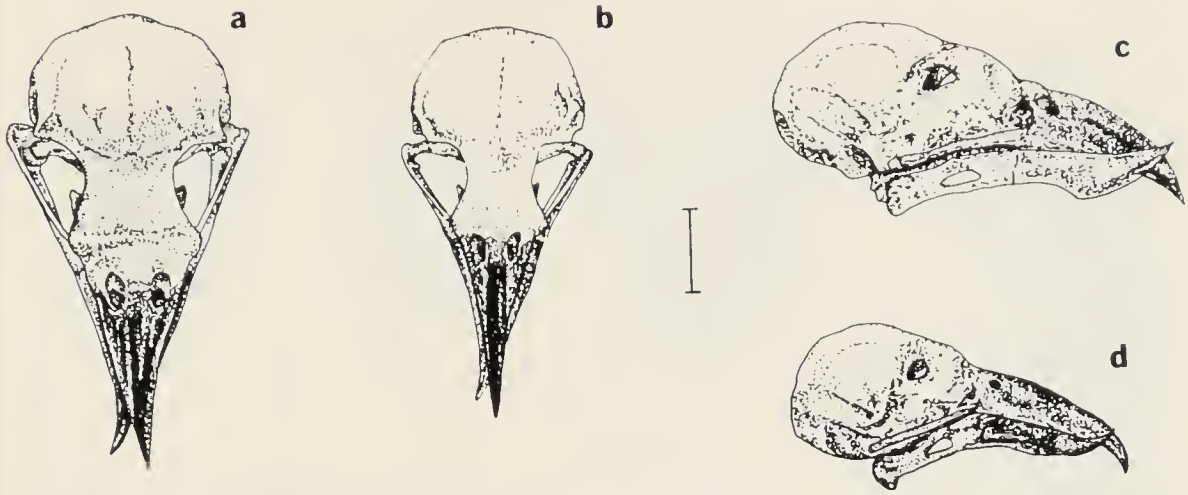

FIG. 1. Dorsal (a, b) and lateral (c, d) views of the bills and skulls of Red and White-winged Crossbills. Note the smaller and more slender bill of the White-winged Crossbill (b, d) as compared to the Red Crossbill (a, c). The bar equals 1 cm.

where Red Crossbills were housed. Crossbills were provided with fresh conifer branches every 3–7 days, with daily supplements of water, vitamins, grit, salt, limited quantities of commercial sunflower and thistle seeds, and conifer cones. Fresh cones were usually available to crossbills in the aviary. During the 6 months the experiments were conducted, most of the crossbills' diet consisted of conifer seeds, which the crossbills had to extract from cones.

Data were gathered for both species foraging on seven species of conifers (Fig. 2). The cones of these conifers represent both the size and structural variation of conifer cones found in northeastern North America. I chose cones that represented what I considered the average sizes and shapes for each species of conifer, except for pitch pine (*P. rigida*) whose cones appeared smaller than average. Every attempt was made to minimize structural variation among individual cones for each species, and the cone structure and seed number for each cone stage. Cones of the same species (usually from the same tree) and ripeness were given to both species of crossbills on the same day. Thus foraging efficiency differences between crossbills on a given conifer are largely attributable to differences between the crossbills rather than to differences among individual trees or cones.

Conifer cones vary in structure depending on ripeness: Cone scales were initially closed but eventually had wide gaps between them. After the scales spread apart (dehisce), seeds fall out. For each conifer, I selected cones with mature seed representing up to seven stages between closed cones to open cones. These cone stages, ranked in order of ripening phenology, are: (1) closed; (2) closed to a few scales opening; (3) a few to up to half of the scales opening; (4) all to nearly all scales open; (5) 14–22 seeds in open cone; (6) 7–13 seeds in open cone; and (7) 3–6 seeds in open cone. Stages not used were stage 1 for eastern hemlock (*Tsuga canadensis*), stage 2 for pitch pine, and stage 5 for jack pine (*P. banksiana*). Closed cones of each conifer species were gathered and either given to the crossbills within the next two to three days or they were stored in a refrigerator (2°C) until used. Open cones were obtained from either closed cones that were dried over a heat source or open cones that were gathered in the field. In both cases the open cones appeared similar. I created cones with progressively fewer seeds either by shaking open cones or by haphazardly removing seeds with forceps, or both. I placed seeds in empty cones of pitch pine to create its two cone stages with the fewest seeds. This was necessary because once pitch pine cones open, seeds shed rapidly from the cone.

Dry mass of seed kernels (female gametophyte and embryo) was measured with a Mettler

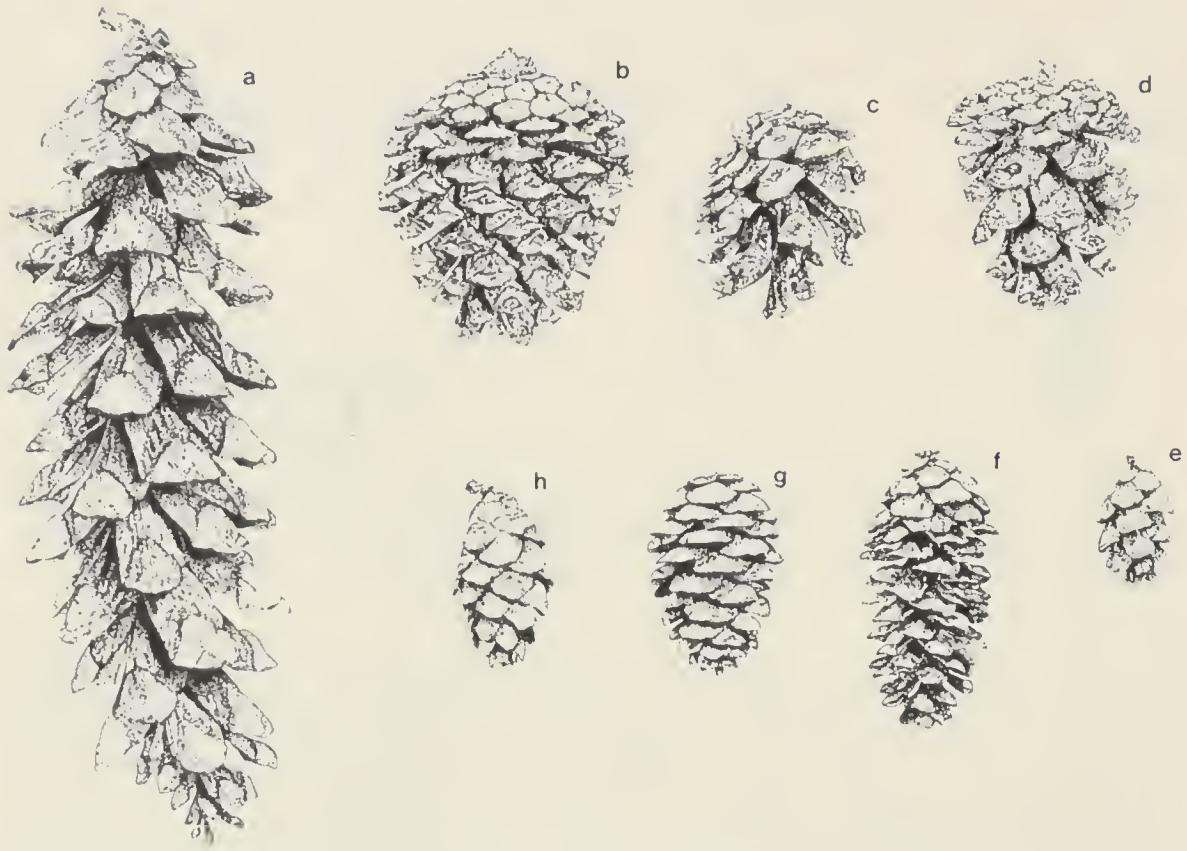

FIG. 2. Open cones of the seven species of conifers used in the experiments (a–c, e–h), plus red pine (d). Conifer cones: a = white pine, b = pitch pine, c = jack pine, d = red pine, e = eastern hemlock, f = white spruce, g = red spruce, and h = black spruce. The bar equals 1 cm.

balance. Kernels were separated from the seed coats and dried at 60–65°C for 3–8 days, and then weighed. The mean kernel mass for each species was used to compute intake rates (mg kernel ingested/sec). Extensive samples of kernel mass were not made because mass varies relatively little within and between individual trees (Smith 1970; see also Haddon 1982).

Five cone scales from the midsection of mature and air-dried cones from each conifer species were removed and weighed to the nearest 0.1 mg with a Mettler balance. The midsection of a cone has the largest scales (see Fig. 2) and the highest seed concentration (Lyons 1956, pers. obs.). Cone scale width, length, and depth were measured to the nearest 0.1 mm with dial calipers. Scale width was measured at the widest part of the cone scale, and scale length was measured from the distal end of the seed scar to the tip of the scale. Scale depth was measured at the middle of the seed scar. Although these scale measurements are an inadequate characterization of all scales on a cone, they provide relative scale sizes of the different species.

Foraging data were measured for three male White-winged Crossbills and two male and two female Red Crossbills between 3 September 1984 and 11 February 1985. Observations of crossbills foraging on each conifer species lasted up to eight days and were preceded by at least one day of foraging on cones of the respective conifer species. There was no temporal increase in foraging efficiency that might have resulted from learning.

Crossbills were recorded foraging from early morning to early afternoon. They were deprived of seed for >12 h before the experiments. On the day of the experiments, crossbills

were given 2–20 cones, with fewer cones given when total seed mass in the cones was large, and then foraging bouts were timed. Data in related studies demonstrate that feeding rates were usually higher for birds in the presence of other crossbills; therefore, during all timed bouts the other species of crossbill was present on the other side of the hardware cloth partition and at least one other conspecific was usually present in the same section with the bird being tested. A sufficient number of cones was given so that aggressive interactions were minimal.

Crossbills were observed through a one-way glass foraging less than 2 m distant in the same aviary in which they were housed. Foraging bouts were timed from when the bird began prying apart or probing between cone scales to when it finished consuming the last seed it obtained from the cone; crossbills usually did not consume all the seeds in the cones. Most often I counted the number of seeds consumed while timing the whole bout with a stopwatch. In some cases, I recorded both seed-husking times and interseed intervals with a computer programmed as an event recorder. Seed-husking time is the time from when the seed is initially held in the bill until the kernel is swallowed. Interseed interval is the time between the end of husking one seed to the beginning of husking the next seed. Interseed interval was obtained by subtracting mean seed-husking time from mean time per seed. I used a computer to record all bouts for the first cone stage of hemlock, the second cone stage of white spruce, the first three cone stages of black spruce and all cone stages of white pine. In all other cases a stopwatch was used. For conifer species for which I only used a stopwatch to record foraging bouts, I also used the computer to measure seed-husking time during separate bouts. In some cases, when >30 seeds were consumed per cone, I terminated my recording of the bout before the last seed was eaten. This should not affect the results because in cases where 30 or more seeds were consumed per cone there was no correlation between number of seeds obtained per second and the number of seeds consumed (three cone stages of white spruce for each crossbill species; $r = -0.03$ to 0.34; $P > 0.1$ in all six cases). White pine cones have large quantities of pitch covering them; therefore, I also measured time spent removing pitch from the bill and adjacent feathers (e.g., bill wiping) during and immediately following seed extraction, as part of the bout. Measures of travel and search time were not attempted in the laboratory because in the field they usually represent <10% of total foraging time (pers. obs.) and would be difficult to simulate. Foraging bouts and seed husking were timed to the nearest 1.0 and 0.1 sec, respectively. The data presented are from crossbills consuming >20,000 seeds.

For all analyses, an ANOVA was used to determine if individual crossbills differed. In cases where individuals differed, all subsequent analyses that included those cases were based on the means of each individual. In cases where individuals did not differ, analyses were based on individual samples from each bird. To determine if interseed intervals and kernel intake rates differed both between crossbills and for each crossbill on the different conifers, an ANOVA was employed with cone stage as a covariate.

RESULTS

Foraging Behavior

When feeding, crossbills usually orient themselves so that their lower mandible is directed parallel to the long axis of the cone scales (Fig. 3). The lower mandible curves slightly laterally, either to the left or right, whereas the upper mandible is directed more straightforward (Fig. 1). The tip of the lower mandible is placed against a cone scale (I call this scale the distal scale because it is toward the distal end of the cone relative to

FIG. 3. A dorsal view of the head and mandibles of a Red Crossbill separating conifer cone scales. A median longitudinal section of the cone is illustrated. Note that the upper mandible rests parallel with the basal cone scale (b) and that only the tip of the lower mandible is positioned on the distal cone scale (d). Arrows point in the approximate directions in which forces are exerted by the mandibles. Seeds (4) are hatched, and the cone axis runs nearly perpendicularly to the "basal scale" in the figure. See text for further description.

the scale against which the upper mandible pushes [Fig. 3]). To create a gap between cone scales, the decurved and pointed upper mandible slides between the scales in a biting motion, often tearing tightly closed scales. After an initial gap is created, the jaws spread sideways (i.e., the lower jaw is abducted laterally in the direction that its tip points) so that the lateral surface of the upper mandible pushes the more basal scale away from the cone axis while the lower mandible presses against the distal scale (Fig. 3). Lateral abduction of the lower jaw takes place while the bill is slightly open (gaped). Lateral spread of the jaws widens and deepens the gap between the scales. The upper mandible again is driven deeper between the scale gap, and then the mandibles further separate the adjacent cone scales with a lateral abducting motion. The lower mandible pivots on the distal cone scale, whereas the upper mandible remains parallel with the more basal scale against which it pushes (Fig. 3). The upper mandible is relatively more active than the lower mandible, which often remains at the same site on the distal scale if the upper mandible has not penetrated very far. The tip of the laterally curved lower mandible provides a brace against the distal scale, providing a stable foundation for movement of

TABLE 2

SEED KERNEL MASSES AND HUSKING TIMES FOR WHITE-WINGED AND RED CROSSBILLS

	Kernel mass (mg)	Seed-husking time (sec)		P^e
		White-winged Crossbill	Red Crossbill	
White spruce	1.6 ± 0.05[a] (26)[b]	1.1 ± 0.05[c] (1089)[d]	2.2 ± 0.11 (873)	<0.05
Black spruce	1.6 ± 0.05 (30)	0.9 ± 0.03 (401)	1.9 ± 0.06 (567)	<0.005
Tamarack	1.6 ± 0.05 (30)	1.2 ± 0.09 (212)	1.7 ± 0.07 (272)	NS
Red spruce	1.7 ± 0.06 (30)	0.9 ± 0.08 (58)	2.4 ± 0.09 (68)	<0.05
E. hemlock	2.1 ± 0.06 (20)	2.5 ± 0.15 (245)	1.6 ± 0.09 (184)	<0.05
Pitch pine	2.6 ± 0.12 (20)	2.0 ± 0.12 (55)	1.8 ± 0.04 (97)	NS
Jack pine	2.9 ± 0.08 (20)	1.6 ± 0.29 (19)	1.7 ± 0.06 (61)	NS
Red pine	5.9 ± 0.16 (30)	5.0 ± 0.33 (20)	2.6 ± 0.12 (156)	<0.005
White pine	13.7 ± 0.33 (19)	8.4 ± 0.40 (337)	2.6 ± 0.08 (587)	<0.005

[a] $\bar{x}$ ± SE.
[b] Sample sizes for kernel mass are number of kernels.
[c] Seed-husking times are based on the means for each of three White-winged Crossbills and four Red Crossbills.
[d] Because there are significant differences among individuals for at least one species of crossbill on all conifers but red pine (ANOVA, $P < 0.05$), pair-wise comparisons are based on the means of each individual (i.e., N equals 3 for White-winged Crossbills and 4 for Red Crossbills). The N presented is the total number of seeds husked.
[e] Probability of a species difference using ANOVA.

the upper mandible. The consistency with which crossbills place their lower mandible against the distal scale has been noted previously (e.g., Tordoff 1954, Newton 1967) and is due to the different functions each mandible performs.

When the seed is exposed, the tongue is protruded and its spoon-shaped tip carries the loose seed to the bill to be husked. With thin-scaled cones the upper mandible is often used to hook the seed from between the scales, whereas on thick-scaled (or dry) cones, lateral abducting forces alone are usually sufficient to expose the seeds.

Crossbill handling behavior consists of two components: (1) extraction of seeds from cones (interseed interval or ISI) and (2) seed husking. The two components are analyzed separately below as ISI is mainly affected by cone structure, which varies with cone stage, whereas seed-husking time is influenced mainly by seed structure and size, which varies little with cone stage.

Seed Husking

White-winged Crossbills husked the smaller seeds of the spruces more rapidly than did Red Crossbills, whereas the converse was true on the larger seeds of the pines and hemlock (Table 2). Seed profitability, Y (mg kernel ingested/sec), remained constant for all seed sizes (X) for White-winged Crossbills ($Y = 1.52 - 0.002X$, df = 7, $r^2 = -0.0004$, $P = 0.96$),

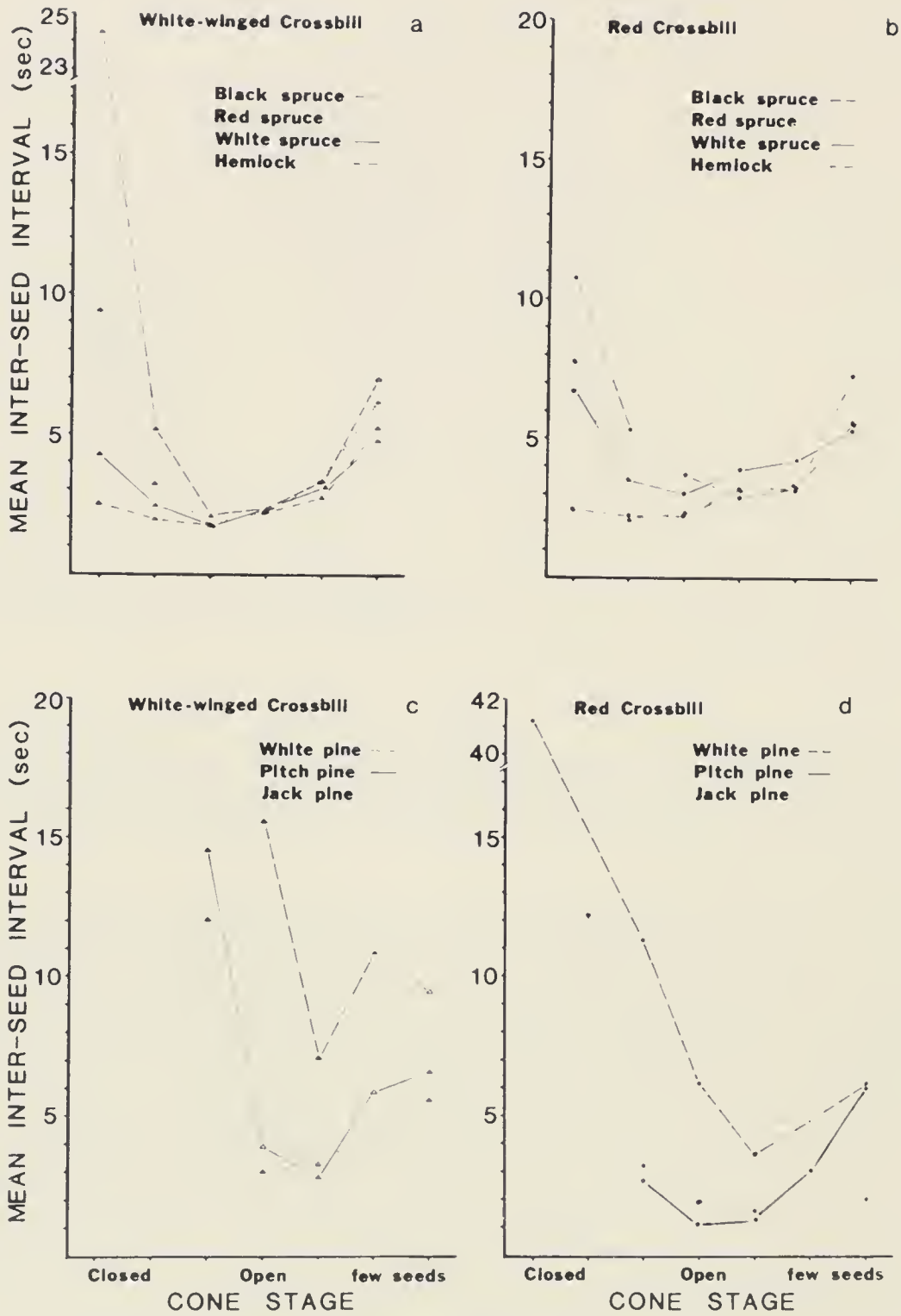

FIG. 4. Interseed intervals for crossbills foraging on different cone stages. (a) White-winged Crossbills foraging on hemlock and spruce. (b) Red Crossbills foraging on hemlock and spruce. (c) White-winged Crossbills foraging on pine. (d) Red Crossbills foraging on pine. Samples sizes are given in Figs. 5 and 6.

TABLE 3

CHARACTERISTICS OF SCALES FROM THE MIDDLE SECTION OF THE CONES OF EACH CONIFER SPECIES USED IN THE FORAGING EXPERIMENTS (CONES WERE MATURE, OPEN AND AIR-DRIED)[a]

	Scale size (mm)			
	Width[b]	Length[c]	Depth[d]	Mass (mg)
E. hemlock	5.9 ± 0.21[e]	4.8 ± 0.25	0.8 ± 0.04	10.3 ± 0.32
White spruce	9.0 ± 0.23	7.0 ± 0.68	0.8 ± 0.05	14.6 ± 1.68
Red spruce	11.2 ± 0.16	8.8 ± 0.39	1.1 ± 0.04	37.5 ± 0.56
Black spruce	7.6 ± 0.39	7.6 ± 0.18	1.5 ± 0.07	36.8 ± 3.41
Jack pine	7.8 ± 0.47	15.1 ± 0.74	0.9 ± 0.04	108.8 ± 13.52
Pitch pine	12.2 ± 0.45	13.5 ± 0.20	1.5 ± 0.23	126.5 ± 8.45
White pine	15.1 ± 0.21	22.4 ± 0.16	2.3 ± 0.33	182.6 ± 5.02

[a] N = 5 for all measurements.
[b] Greatest width of scale.
[c] Distance from distal end of seed to cone scale tip.
[d] Depth of scale at middle of seed scar on scale.
[e] Mean ± SE.

but increased with seed size for Red Crossbills ($Y = 0.34 + 0.36X$, df = 7, $r^2 = 0.98$, $P < 0.0001$).

Interseed Interval

Hemlock and spruce.—ISI's were largest and their differences among hemlock and spruce greatest when the cones were closed or when few seeds remained in the cones (Fig. 4A, B). When cones of hemlock and the three species of spruce were open and filled with seeds, the ISI's for White-winged Crossbills were very similar (Fig. 4A). As cone scale size increased, the effect on ISI of cones being closed increased. Cone scale mass and depth increased in the following progression: hemlock, white spruce, red spruce (*P. rubens*), and black spruce (Table 3, Fig. 2). For White-winged Crossbills foraging on the first cone stage of hemlock and the three spruces (N = 4), ISI was most highly correlated with scale depth ($r = 0.99$), then mass ($r = 0.76$), length ($r = 0.48$), and width ($r = 0.03$). The relative importance of scale thickness in impeding White-winged Crossbills can be seen by comparing red spruce to black spruce. Red spruce has wider and longer cone scales than does black spruce. Black spruce seeds, however, were generally less accessible than those of red spruce, in large part because black spruce has thicker cone scales and was thus more resistant to forces exerted by crossbills.

The effect of cone stage, with conifer species the covariate, was significant for both White-winged Crossbills ($F = 58.1$, df = 5,62, $P < 0.0001$) and Red Crossbills ($F = 50.2$, df = 5,85, $P < 0.0001$) (Fig. 4A, B). The

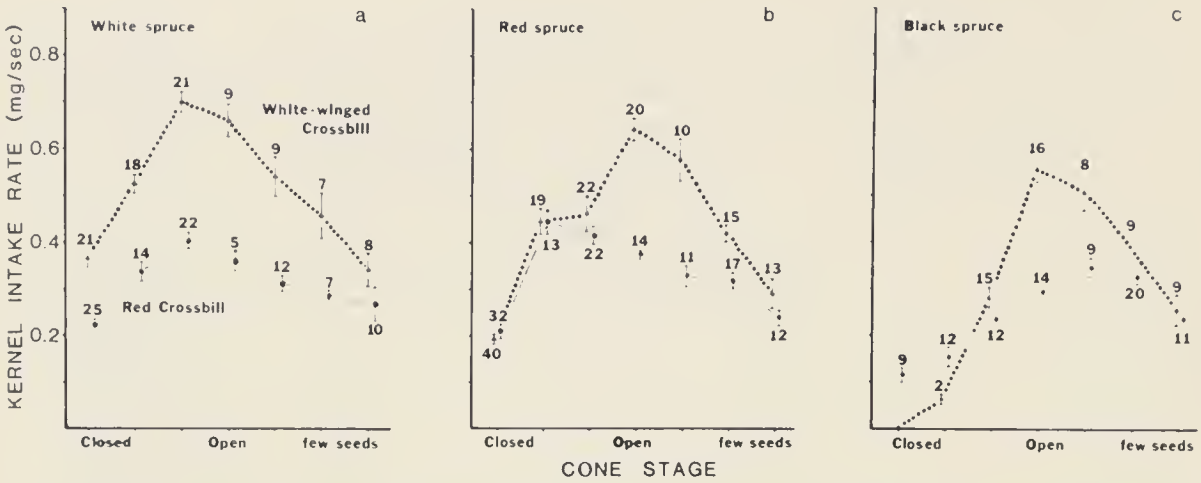

FIG. 5. Mean (±SE) kernel intake rates of White-winged Crossbills (triangles connected by dotted lines) and Red Crossbills (closed circles connected by dashed lines) foraging on cones of three species of spruce. Cone ripening progresses to the right. Sample sizes are the number of cones; total number of seeds was >3000 for each crossbill species.

one cone stage for which White-winged Crossbills had lower ISI's than Red Crossbills was when cones were open and nearly full of seeds.

Pine.—Red Crossbills extracted seeds more rapidly than did White-winged Crossbills from the cones of jack pine ($F = 7.7$, df = 1,25, $P = 0.01$), pitch pine ($F = 12.6$, df = 1,27, $P < 0.002$), and white pine ($F = 18.1$, df = 1,16, $P < 0.001$), and for each pine species Red Crossbills extracted seeds from one to three earlier cone stages than did White-winged Crossbills (Fig. 4C, D). For both crossbill species, the differences in ISI was greater among pines ($F = 8.1$, df = 2,31, $P = 0.002$ for White-winged Crossbills; $F = 12.1$, df = 2,46, $P < 0.0001$ for Red Crossbills) than among hemlock and spruces ($F = 2.0$, df = 3,64, $P = 0.12$ for White-winged Crossbills; $F = 2.3$, df = 3,87, $P = 0.08$ for Red Crossbills). This was apparently related to the greater absolute differences in cone scale structure and mass among pines than among hemlock and spruces (Table 3, Fig. 2). For both crossbill species, ISI was greater on white pine than on either jack pine or pitch pine; however, the ISI for the latter two pines was similar for both White-winged Crossbills ($F = 0.03$, df = 1,24, $P = 0.86$) and Red Crossbills ($F = 0.14$, df = 1,32, $P = 0.71$). The thicker and longer cone scales of white pine (Table 3, Fig. 2) probably caused the higher ISI's. These data imply that (1) White-winged Crossbills were impeded more by the relatively long and massive pine cone scales than were Red Crossbills, and (2) the bill of the Red Crossbill, as compared to that of the White-winged Crossbill, appeared to be particularly well adapted for extracting seeds that were relatively inaccessible.

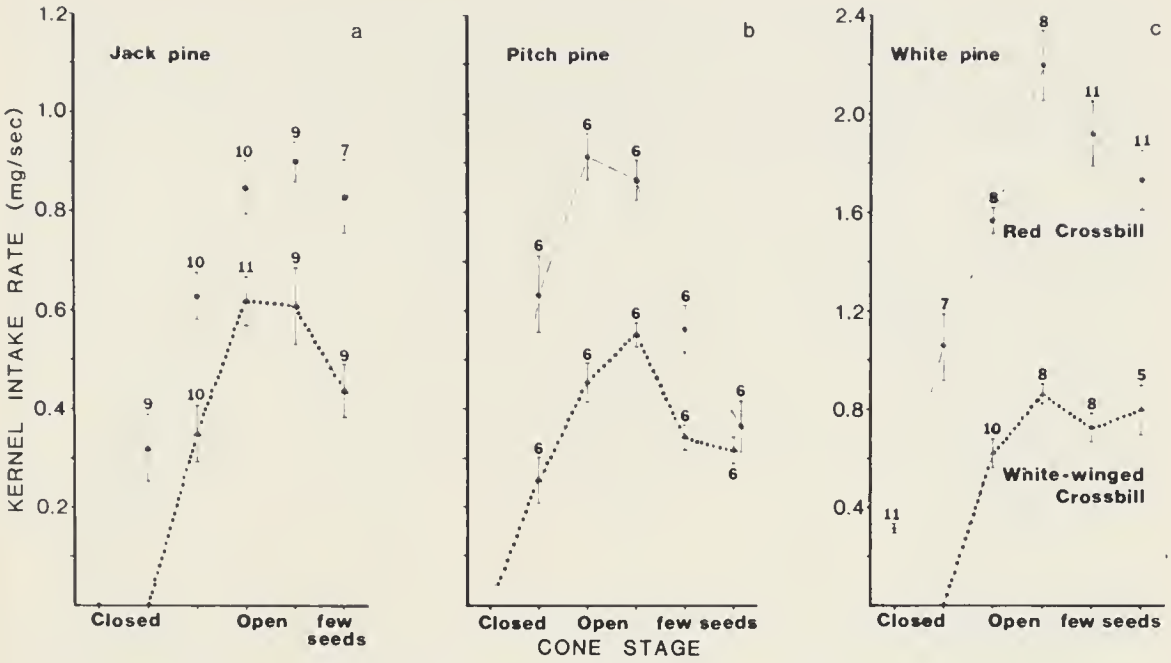

FIG. 6. Mean (±SE) kernel intake rates of White-winged and Red crossbills foraging on cones of three species of pines. Symbols as in Fig. 5. Total number of seeds was >1400 for White-winged Crossbills and >2600 for Red Crossbills.

Intake Rates

In both species profitability increased as cones opened, then declined as seeds were shed from the cones of all seven conifer species (Figs. 5 and 6) as a result of variation in seed accessibility (Fig. 4). Because ISI was both more variable and usually greater at any given cone stage than seed-husking time, ISI contributed relatively more to patterns of profitability. On most conifer species, individuals within each crossbill species did not differ significantly in intake rates (Table 4).

Hemlock and spruce.—Red Crossbills had slightly higher intake rates on hemlock than did White-winged Crossbills ($F = 4.9$, df = 1,39, $P = 0.03$). On average, White-winged Crossbills had slightly lower intake rates, and Red Crossbills had slightly higher intake rates on hemlock than their respective intake rates on white spruce (see Fig. 5A). White-winged Crossbills were more efficient than Red Crossbills on white spruce ($F = 41.5$, df = 1,42, $P < 0.0001$), red spruce ($F = 55.4$, df = 1,246, $P < 0.0001$), and black spruce ($F = 9.7$, df = 1,135, $P < 0.005$).

On closed white spruce cones, White-winged Crossbills foraged more efficiently than did Red Crossbills (Fig. 5A), but the foraging efficiency of White-winged Crossbills as compared to that for Red Crossbills was similar on the first and second cone stages of red spruce (Fig. 5B), and it was

TABLE 4
ANOVA FOR DIFFERENCES AMONG THREE WHITE-WINGED CROSSBILLS AND FOUR RED CROSSBILLS WHEN FORAGING ON SEVEN SPECIES OF CONIFERS (CONE STAGE WAS A COVARIATE)

	df	*F*-ratio	*P*
White-winged Crossbill			
Eastern hemlock	2,146	2.6	0.076
White spruce	2,89	0.9	0.404
Red spruce	2,139	1.4	0.244
Black spruce	2,53	0.1	0.932
Jack pine	2,35	7.2	0.002
Pitch pine	2,26	0.8	0.442
White pine	1,32	0.4	0.516
Red Crossbill			
Eastern hemlock	3,146	19.6	0.0001
White spruce	3,90	6.9	0.0003
Red spruce	3,135	0.9	0.435
Black spruce	3,82	1.4	0.258
Jack pine	3,41	0.6	0.628
Pitch pine	2,26	2.1	0.138
White pine	3,36	1.6	0.202

less on the first two cone stages of black spruce (White-winged Crossbills could not extract seed from the first cone stage) (Fig. 5C). Cone scale depth and difficulty of extracting seeds from closed cones increased from white to red to black spruce.

White-winged Crossbills were more efficient than Red Crossbills when spruce cones were open and full of seeds (Figs. 5A–C), because White-winged Crossbills required less time to handle spruce seed (Table 2) and secure them from the cones (Fig. 4). White-winged Crossbill and Red Crossbill intake rates converged when few seeds remained in spruce cones. The few remaining seeds were difficult to extract because they were usually secured between the most closed cone scales.

Pine.—Red Crossbills had higher intake rates than White-winged Crossbills did on jack pine ($F = 14.1$, df = 1,29, $P < 0.001$), pitch pine ($F = 96.5$, df = 1,50, $P < 0.0001$), and white pine ($F = 276.2$, df = 1,74, $P < 0.0001$) (Figs. 6A–C). Neither crossbill species extracted seeds from closed jack and pitch pine cones; crossbills require a gap between the scales into which they slide their bills to separate the scales. The similarity between the intake rates of White-winged and Red crossbills on the last two cone stages of pitch pine, in contrast to those on the other pines, is probably

an artifact of my methods for creating these two cone stages for pitch pine (see Methods). Red Crossbills removed seeds from closed white pine by shredding the relatively soft cone scales. Red Crossbills often removed pieces of white pine seed kernel from the shredded cones, rather than the whole seed. As the complete kernel was not always removed, the intake rate was over-estimated for closed white pine cones; for estimates of profitability I assumed whole kernels were consumed. Red Crossbills extracted seeds from an earlier cone stage of jack pine than pitch pine because it was apparently easier to separate the thinner and less massive cone scales of jack pine (Table 3). The second cone stage of white pine was cones with scales just separating; Red Crossbills easily separated the cone scales apart to expose the underlying seeds, but White-winged Crossbills could not.

White-winged Crossbills had higher maximum intake rates when foraging on spruce than on jack and pitch pines, but White-winged Crossbills had their highest intake rates on white pine. However, although all 3 White-winged Crossbills foraged on all other conifers, only 2 of the 3 foraged on white pine cones. The pitch covering the outer surface of the cone apparently deterred the one White-winged Crossbill from foraging. Furthermore, the two individuals that did forage on white pines dropped small pieces of seed kernel that were broken off large kernels. This resulted in lower intake rates for White-winged Crossbills on white pine than is indicated in Figure 6C.

DISCUSSION

Foraging behavior and morphology.—It has long been assumed that small-billed crossbills forage relatively more efficiently on small conifer cones and that large-billed crossbills forage relatively more efficiently on large conifer cones (Griscom 1937; Lack 1944a, b; Southern 1945; Newton 1972). That large-billed crossbills are more efficient on large cones than small-billed crossbills is supported by Niethammer's (1937, cited in Lack 1944b and Newton 1967) observations of the largest billed crossbill, the Parrot Crossbill (*L. pytyopsittacus*), foraging more efficiently on pine cones than the Red Crossbill. My data support these contentions and observations. White-winged Crossbills have smaller bills than Red Crossbills in terms of depth, length, and width (Table 1, Fig. 1). These morphological differences result in differences in foraging efficiency.

Bill depth influences biting force (Bock 1966). Deep bills are usually thought to be critical for husking hard seeds (Grant 1981). Red Crossbills have deeper bills (Fig. 1) and, in fact, husk larger, harder seeds more efficiently than do White-winged Crossbills. The width of the palatine grooves of the horny palate is also essential for securing seeds in the bill

while seeds are husked (Ziswiler 1965, Newton 1967). The White-winged Crossbill's slender upper mandible has relatively narrow palatine grooves (pers. obs.), which likely is one reason that White-winged Crossbills husk small seeds more efficiently than do Red Crossbills. As seed size increases, White-winged Crossbills have increasing difficulty mandibulating seeds and cracking seed coats; therefore, seed-husking time increases. The wider palatine grooves and deeper bills enable Red Crossbills to crack and remove seed coats from large seeds efficiently.

White-winged Crossbills are most efficient at extracting seeds from between thin and relatively short cone scales, especially when the cones are at least partially open. The slender upper mandible of the White-winged Crossbill is well suited both for sliding rapidly between and for hooking seeds free from between the thin scales of spruce and tamarack cones. White-winged Crossbills rely less on powerful lateral abduction of their mandibles to separate adjacent cone scales to expose seeds than do Red Crossbills. However, White-winged Crossbills are affected more by differences in cone structure than are Red Crossbills. As cone scale mass increases, from hemlock to white pine, the range of cone stages for which White-winged Crossbills have high intake rates diminishes.

The deeper and wider bill of the Red Crossbill enables them to harvest seeds from a wide range of cone structures, including seeds secured between thick cone scales. Greater depth throughout most of the bill's length should enable Red Crossbills to exert a more powerful bite at the tip of their mandibles than can White-winged Crossbills. A powerful bite is essential to creating gaps between cone scales without openings; gaps between the scales are necessary for the mandibles to be inserted between the scales. The deeper and wider bill of the Red Crossbill enables it to separate the closed cone scales of pines and black spruce more efficiently than White-winged Crossbills.

As the length and thickness of cone scales increase, greater bill strength and probing ability are required to secure seeds. A deep and wide bill provides power, but greater probing capacity requires either a long bill or a protrusible tongue. Red Crossbills have only slightly longer bills than do White-winged Crossbills, and, compared to differences in other bill dimensions, Red Crossbills have relatively short bills that are proportional to the cube of their body mass (Table 1). Red Crossbills, and probably other large-billed crossbills such as the Parrot Crossbill, have increased probing ability by evolving relatively long tongues. The ratio of tongue length (tip of fleshy part of tongue to posterior tip of basihyal for two dried tongues of each species) to bill length is 1.00 and 0.67 for Red and White-winged crossbills, respectively. (See Benkman 1985 for more detailed discussion.)

Conifer use, distribution, and bill structure.—The relative intake rates on the different conifers underlie the differences in distribution and conifer use between the two species of crossbills. In nature, crossbills forage mainly on the most profitable conifer species (Benkman, in press). White-winged Crossbills occur primarily in habitats dominated by spruce, and when in mixed conifer forests, they rarely forage on pines. Red Crossbills are found most often in habitats characterized by pines and, when in mixed conifer forests, they forage mostly on pine.

Bill structure is best suited for using efficiently those foods available during periods of greatest food limitation. For example, studies on Galápagos finches have shown that natural selection on bill structure is greatest during periods of extreme food limitation (Boag and Grant 1981, Price et al. 1984), and that bill structure is most strongly related to diets during the periods of food limitation (Grant 1986). Diet overlap between crossbills is often 100% in late summer when both species forage on white spruce, food abundance is high, and increasing and when crossbills nest. Diet overlap declines in early autumn, and it is virtually nonexistent by late winter (Benkman, in press).

Black spruce is the one conifer in habitats occupied by White-winged Crossbills that consistently holds seeds in its cones during winter (see Fowells 1965). Most of the seeds, however, are in closed cones and are inaccessible to White-winged Crossbills (Fig. 5C). Although a more robust bill and more massive jaw musculature, as found in the Red Crossbill, would improve foraging efficiency on closed black spruce cones, intake rates would still be inadequate to meet energy demands; to survive in winter a White-winged Crossbill requires an estimated minimum intake rate of 0.2 mg/sec (Benkman, in press; compare this estimate to the rates in Fig. 5C). This would be especially true if body mass was increased to provide more power. Instead, White-winged Crossbills have apparently evolved to harvest the more accessible, but less abundant seeds in the slightly open to open black spruce cones. The slender bill is particularly efficient at sliding into the narrow gaps between black spruce cone scales (Fig. 5C; note also the narrow gaps in the open black spruce cone in Fig. 2). Red Crossbills, on the other hand, rely on the few remaining well-secured seeds in the cones of pines such as those of red pine (*P. resinosa*; see Fig. 2). The powerful bill of Red Crossbills is required to efficiently extract these seeds. For example, in January 1985 in Algonquin Provincial Park, Ontario, Red Crossbills had an intake rate on red pine ($\bar{x} = 0.73 \pm 0.06$ mg/sec [SE], N = 66 bouts) that was 10 times greater than that for White-winged Crossbills ($\bar{x} = 0.07 \pm 0.03$ mg/sec, N = 8 bouts).

A corollary to this argument is that, because natural selection on foraging efficiency is greatest in late winter when White-winged Crossbills forage

on black spruce and Red Crossbills forage on red pine, the variation in foraging efficiency among individuals foraging on these conifers should be less than on other conifers. There are no differences among individual White-winged Crossbills when foraging on black spruce or among Red Crossbills foraging on jack pine (Table 4); jack pine has the most similar cone to red pine (Fig. 2). Individuals within both species of crossbills, however, do differ when foraging on some of the conifers they use infrequently or during periods of high food abundance, and that differ substantially in structure from the cones used in late winter (e.g., jack pine for White-winged Crossbills, hemlock and white spruce for Red Crossbills). Although the number of individual birds studied was quite small, the pattern of individual variation is provocative. A careful laboratory study on many individuals combined with detailed field work could provide a method to indirectly investigate patterns of selection even when individuals cannot be followed over long periods of time in the field.

Extrapolation from laboratory to field.—The different cone stages given to crossbills represent most of the range of conifer cone stages that crossbills may forage on in northeastern North America. The one exception is during late June, July, and August, when crossbills forage on immature seeds in closed cones of red and white spruce and hemlock (Benkman, in press). In these cases, seed accessibilities differ little from those on closed cones in late August and September (pers. obs.), when the cones I used were gathered, although seed mass (and nutritive and caloric value) is less (e.g., Dickmann and Kozlowski 1969).

Other than for the closed-cone stages, specific dates cannot be assigned to most cone stages because ripening phenologies and seed release vary annually (Cayford 1964, Graber 1971), and even geographically (Benkman, in press). Furthermore, cone-crop size can vary by orders of magnitude from year to year (Fowells 1965), and during years of good cone crops seed profitability is usually greater and remains higher for longer periods than during poor cone crop years (Benkman, in press). Because of this variation, quantitative predictions of conifer seed profitability are tenuous.

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The Hawk Mountain Sanctuary Association is accepting applications for its eleventh annual award for raptor research. To apply for the $750 award, a student applicant should submit a brief description of his or her research program (five pages maximum), a curriculum vitae, and two letters of recommendation to Stanley E. Senner, Executive Director, Hawk Mountain Sanctuary Association, Rte. 2, Kempton, Pennsylvania 19529. The deadline for applications is October 15, 1987. The Association's board of directors will make a final decision early in 1988. Only students in degree-granting institutions are eligible to apply; both undergraduate and graduate students may apply. The award will be granted on the basis of a project's potential to improve understanding of raptor biology and its ultimate relevance to the conservation of North American raptor populations.

Wilson Bull., 99(3), 1987, pp. 369–376

GEOGRAPHIC UNIFORMITY IN SONGS OF THE PROTHONOTARY WARBLER

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ABSTRACT.—Oscine songs, which are typically imitated from adult conspecifics, usually vary geographically, but here we document a surprising lack of geographic variation in the songs of the Prothonotary Warbler (*Protonotaria citrea*). A typical song of this species consists of 4 to 14 repeated syllables of one type. Using cluster analysis, we showed that the geographic origins of the similar songs within the state of Texas were closer together than were the locations of song pairs chosen at random. But this statistical demonstration of geographic patterning within Texas was overshadowed by the lack of broad geographic variation: a given Texas song was no more likely to be more similar to another Texas song than to a song from distant portions of eastern North America. How a songbird species can maintain such geographic uniformity in a presumably learned song raises questions about our understanding of the flexibility provided by imitation during song ontogeny. *Received 24 Sept. 1986, accepted 22 Jan. 1987.*

Songbirds typically develop their songs through imitation of conspecifics (e.g., Kroodsma 1982), and because dispersal from the site of learning is usually limited, neighborhoods (or larger regions) of males with similar song types occur. Documenting and understanding these patterns of local geographic song variation in different species, which are a consequence of this vocal imitation, has been a major focus of research in avian bioacoustics (e.g., see reviews of Baker 1982, Mundinger 1982, Slater 1983).

Although most workers have concentrated on *differences* in song structure among populations of a given species, others have revealed constant features of songs that occur throughout the geographic range of a species (cf. Becker 1982). Even the casual bird watcher in his travels realizes that general features of songs such as duration, frequency, or tonal quality usually enable unambiguous identification of most species. An increasing number of studies, however, are demonstrating that the repertoire of different sounds (figures, notes, syllables; i.e., the basic building blocks of songs) that are used to construct songs of a given species is quite limited (Shiovitz and Thompson 1970, James 1984, Marler and Pickert 1984). Vocal learning seems to be required for proper development of this fine structure within oscine song (Rice and Thompson 1968, Güttinger 1979, Marler and Sherman 1985); in our preoccupation with identifying song

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dialects, however, we had come to expect that this learned microstructure would be the first feature of songs to vary geographically. Additional study of the geographic uniformity of learned songs could tell us much about the role of genetic and environmental (i.e., learned) factors in song ontogeny (Güttinger 1979, Marler et al. 1981).

Here we present a striking example of how presumably learned songs (see Kroodsma 1982) recur throughout the geographic range of a songbird, the Prothonotary Warbler (*Protonotaria citrea*). The limited evidence that we have for some geographic structuring within our Texas samples is overshadowed by the broad geographic uniformity of the songs over the eastern half of North America.

METHODS

Between 22 April and 13 June 1978, songs of 150 Prothonotary Warblers were recorded at 10 locations in eastern Texas. Of those 150 songs, three were highly unusual for Prothonotary Warblers (Fig. 1, sonograms 1–3) and were therefore excluded from our study of geographic variation. Six males, however, sang "double songs" that included two different syllable types (see RESULTS for additional description of songs). For our geographic analyses, then, we used a total of 153 syllables from songs of 147 Prothonotary Warblers. The 10 recording locations, together with the sample size of the number of different syllable types used in our analyses from each location (N = 153), were as follows: Brazos Bend State Park, Fort Bend County (N = 7); Upper Lake Conroe, Walker County (N = 8); McCardell Lake, Polk County (N = 14); Engeling Wildlife Management Area, Anderson County (N = 17); Ft. Worth Nature Center, Tarrant County (N = 8); Beaumont Unit, Big Thicket National Preserve, Hardin, Jefferson, Orange, and Jasper counties (N = 13); B. A. Steinhagen Reservoir, Tyler and Jasper counties (N = 21); Upper Toledo Bend Reservoir, Shelby and Panola counties (N = 22); Caddo Lake, Marion and Harrison counties (N = 21); and Wright Patman Reservoir, Bowie and Cass counties (N = 22). We recorded songs on Ampex 641 tape at 19 cm-sec^{-1} with a Uher 4000 Report IC and used a Dan Gibson P650 parabolic microphone. The original recordings have been deposited in the Texas Bird Sound Library, Division of Life Sciences, Geology, and Geography, Sam Houston State University.

We obtained an additional 39 recordings of Prothonotary Warblers from the Cornell Library of Natural Sounds, the Borror Laboratory of Bioacoustics of the Ohio State University, and the Florida State Museum at Gainesville. These recordings contained 42 different syllable types; three males sang double songs, but one-half of one double song was unusual (Fig. 1, sonogram 4) and was not included in our cluster analysis. We divided these samples into two geographic regions: the Great Lakes Region (Illinois, Ohio, Ontario) and the southeastern United States (Florida, Georgia, North Carolina, South Carolina).

We graphed a total of 2380 songs on a Kay Elemetrics 6061B Sound Spectrograph with the "wideband" (300 Hz) filter, but chose for analysis only the highest quality sonogram from each male. For each of the 194 syllables analyzed in this study we measured six temporal and six frequency parameters on the second or third from the last repeated syllable in the song (Fig. 2) (see also RESULTS for a more detailed description of the song). These syllables were typically the loudest, and therefore made the clearest print on the sonogram. For the cluster analysis we used the NTSYS program (Euclidean distance) developed by Rohlf and Kishpaugh (1972).

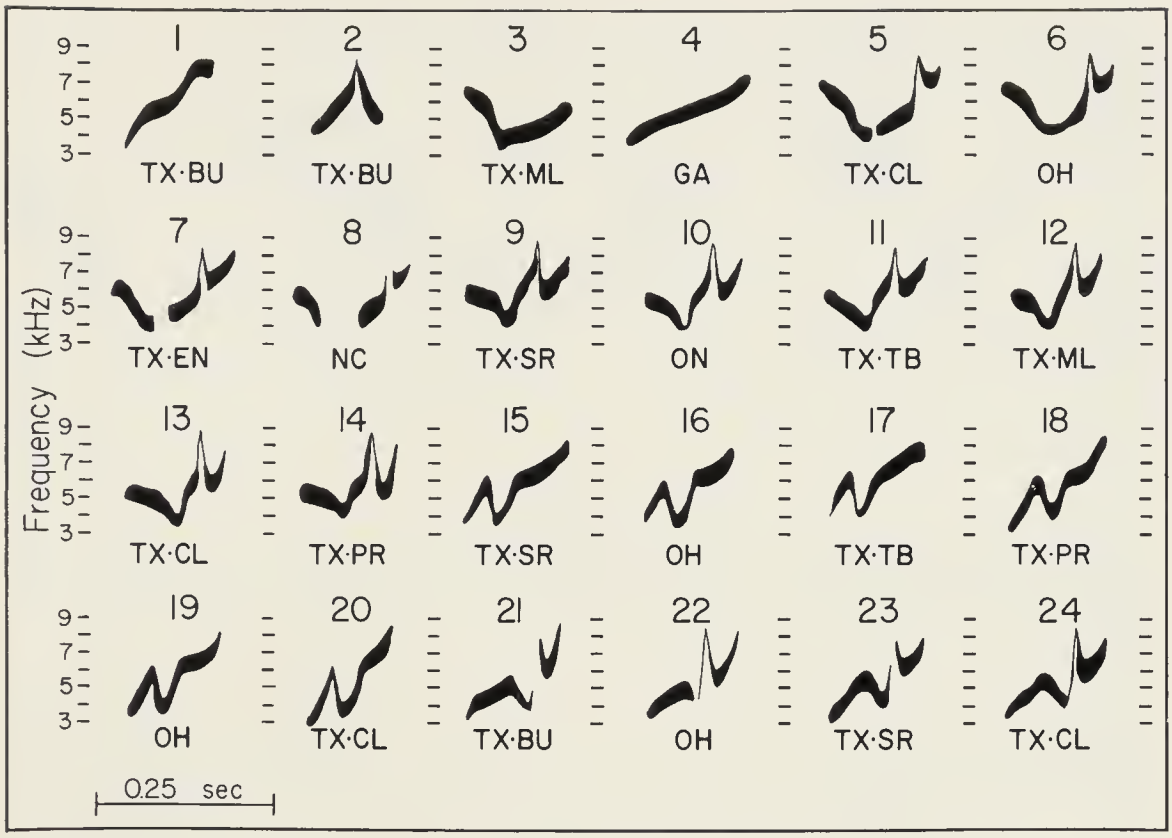

FIG. 1. Examples of atypical syllables omitted from the geographic analyses (1–4) and of syllable patterns that recur throughout the geographic range of the species (5–24). Songs 5–14 are of pattern A, and songs 15–24 are of pattern B (see Fig. 1 and text). State or province locations are provided on the figure; additional information on location and individual is provided for the Texas samples. Exact locations are as follows: (1) Texas, Beaumont Unit Bird 12; (2) Texas, Beaumont Unit Bird 3; (3) Texas, McCardell Lake Bird 3; (4) Georgia, Camp Stephen Foster (Cornell LNS Cut 12); (5) Texas, Caddo Lake Bird 4; (6) Ohio, Winous Pt. (OSU Borror Cut 1444); (7) Texas, Engling WMA Bird 6; (8) N. Carolina, Occoneechee (Univ. Fla. Cut 3); (9) Texas, Steinhagen Reservoir Bird 14; (10) Ontario, Rondeau Park (Cornell LNS Cut 1); (11) Texas, Toledo Bend Bird 9; (12) Texas, McCardell Lake Bird 14; (13) Texas, Caddo Lake Bird 14; (14) Texas, Patman Reservoir Bird 3; (15) Texas, Steinhagen Reservoir Bird 5; (16) Ohio, Winous Pt. (Borror Cut 1068); (17) Texas, Toledo Bend Bird 7; (18) Texas, Patman Reservoir Bird 9; (19) Ohio, Winous Pt. (Borror Cuts 7581, 7593); (20) Texas, Caddo Lake Bird 3; (21) Texas, Beaumont Unit Bird 8; (22) Ohio, Shreve (Borror Cut 6941); (23) Texas, Steinhagen Reservoir Bird 2; (24) Texas, Caddo Lake Bird 1. In our cluster analysis, for example, syllable 5 (from a Texas song) was more similar to syllable 6 (from Ohio) than to any other syllable in our sample. A list of illustrated syllable pairs in which the first listed (e.g., 5) is more similar to the second listed (e.g., 6) than to any other syllable in the sample follows: 5, 6; 7, 8; 9, 10; 11, 10; 12, 10; 13, 14; 14, 13; 15, 16; 17, 15; 18, 19; 20, 18; 21, 22; 23, 24; 24, 23.

RESULTS

Songs of the Prothonotary Warbler.—The song of a Prothonotary Warbler usually consisted of a series of 4 to 14 repeated syllables of a single type, which generally increased in amplitude from the beginning to the

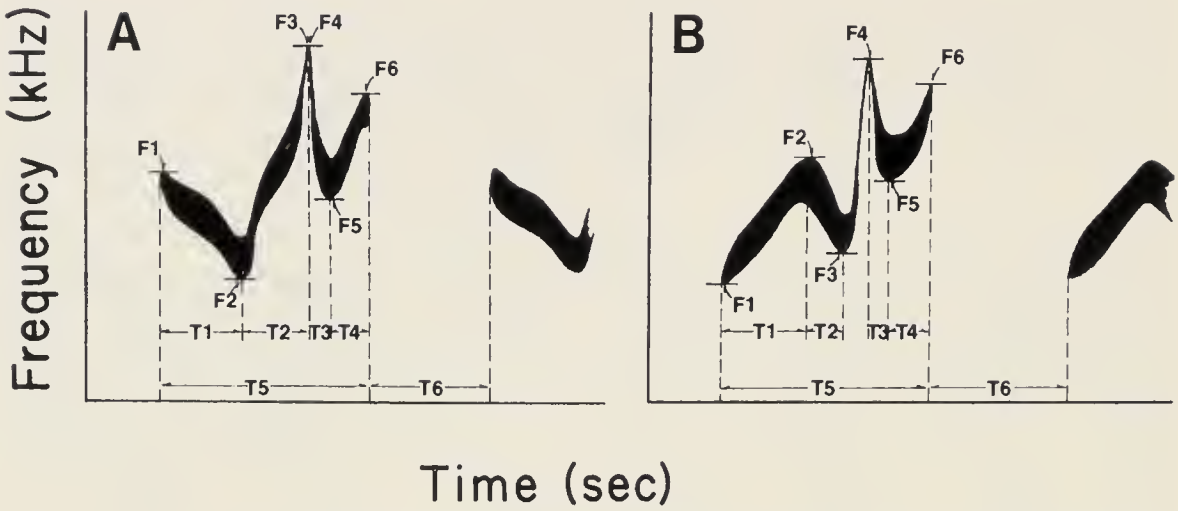

Fig. 2. An illustration of the 12 morphometric measurements on two representative syllable patterns (A and B) found in songs of the Prothonotary Warbler. F1–F6 are frequency measurements, T1–T6 temporal measurements.

end of the song (see sonograms of entire songs in Borror and Gunn 1985). Songs of a given male were stable over time; we recorded three color-banded males during two consecutive months of the same breeding season and one of these banded males in successive years. We could detect no change in the songs of these males.

Nine of 189 males in this study sang a more complicated "double" song that consisted of two series of distinctly different syllable types. Most of the time (60% of all songs), however, even these males sang a simpler song with only one, and usually only the first (8 of 9 males), syllable pattern.

Careful inspection of the sonograms revealed that there were two basic forms of syllables in use by the males (Figs. 1, 2). Both forms were modulated in frequency, but one form (A) initially decreased in frequency while the other (B) initially increased in frequency. In Texas both syllable forms occurred at all locations (frequency of occurrence of "A" syllables ranged from 29% to 68% of the sample, with a median of 55%), and overall there was nearly a 1:1 (actually A:B, 99:95) ratio of these two syllable forms in our analyzed sample of 194 syllables.

Geographic variation in songs.—We found recurrences of particular syllable types of the Prothonotary Warbler throughout the geographic range of the species (Fig. 1) (see also Borror and Gunn 1985). These recurrences, moreover, were so frequent that we could find no patterns of geographic variation in syllable types of this warbler in eastern North America. We used the matrix of phenetic distances provided by the cluster analysis program to determine the most similar syllable type to each of the 194 syllable types in our sample. We found that 29 of 153 Texas syllables were actually more similar to syllables from the Great Lakes or

Southeastern regions than they were to other syllables from Texas; this value was clearly not different from the 32.5 that we would have expected by chance, based only on sample sizes. When we analyzed syllables from the Great Lakes and Southeastern region separately, we found the same result: there was no tendency for syllable types that were most similar to each other to occur in the same geographic region.

When we restricted our analyses to Texas samples, we did find some evidence that the syllables most similar to each other also tended to occur closer together geographically. Thus, in Texas there was a tendency for syllable types that were most similar to each other to occur at the same geographic location ($\chi^2 = 2.73$, df = 1, $P = 0.1$). The most similar pairs of syllables were actually recorded from locations separated by a median distance of 178 km, but syllable pairs chosen at random were from locations that were 202 km apart (difference was statistically significant; 2-tailed Mann-Whitney U-test, $n_1 = n_2 = 153$, $P = 0.002$). Because this warbler lives in floodplain habitats that are relatively isolated, we also tested to see if the most similar songs were likely to occur in the same floodplain; we found no evidence, however, of song type distributions by floodplain ($\chi^2 = 0.20$, df = 1, $P > 0.5$). Thus, neighboring males or males from the same location in Texas did not necessarily have the most similar songs, but the most similar pairs of songs came from locations that were slightly closer together than expected by chance.

DISCUSSION

There is some evidence of local geographic variation within our samples of Prothonotary Warbler songs. Within our Texas samples we found that the geographic locations of the most similar pairs of songs were closer together than were the locations of song type pairs chosen at random. In addition, some preliminary multivariate analyses (χ^2, MANOVA, and canonical analysis; see Bryan 1979 for those analyses and for overall phenograms of data presented in this paper) suggest that some overall variation in temporal or frequency parameters of the songs of this warbler may be explained by geographic location.

What remains most striking about our data, however, are the recurrences of the relatively simple Prothonotary Warbler songs, which consist of a single repeated syllable, throughout the bird's geographic range. A given song from our Texas sample, for example, is equally likely to be most similar to another Texas song, as it is likely to be most similar to a song from Ohio, Ontario, North Carolina, or another distant portion of the geographic range.

Such geographic uniformity of the basic building blocks from which songs are constructed has also been demonstrated in other species. Shiovitz and Thompson (1970) and Emlen (1971) first demonstrated that a

limited number of song elements comprised the songs of the Indigo Bunting (*Passerina cyanea*). Neighboring males learn from each other nearly identical sequences of selected subsets of those song elements (Thompson 1970, Payne 1982), but the basic elements from which the songs are constructed are essentially the same in Michigan, New York, and Kentucky. The congeneric Lazuli Bunting (*P. amoena*) likewise has a limited set of song elements, about 20% of which match elements in the Indigo Bunting (Thompson 1976). Limited repertoires of song elements or reduced geographic variation in at least some song forms also occurs in the Greenfinch (*Chloris chloris*; Güttinger 1977), Yellow Warbler (*Dendroica petechia*; Bankwitz and Thompson 1979), Cirl Bunting (*Emberiza cirlus*; Kreutzer 1979), Chestnut-sided Warbler and Blue-winged Warbler (*Dendroica pensylvanica, Vermivora pinus*; Kroodsma 1981), Yellow-throated Vireo (*Vireo flavifrons*; James 1984), Swamp Sparrow (*Melospiza georgiana*; Marler and Pickert 1984), and Summer and Scarlet tanagers (*Piranga rubra, P. olivacea*; Shy 1984, 1985).

The relative stereotypy of oscine song over broad geographic regions is difficult to explain. Such geographic constancy would be expected in suboscine flycatchers, in which highly stereotyped songs appear to be under strong genetic control (e.g., Kroodsma 1984). But vocal imitation among oscines (including warblers—Kroodsma, unpubl. data) has led to striking examples of song dialects (e.g., Baker 1982) as well as to mimicry of an extraordinary diversity of conspecific, heterospecific, or even nonanimal sounds (see Kroodsma and Baylis 1982 for lists of species). This tremendous potential among some oscines for producing such a diversity of sounds must be limited somehow in other species by forces that preserve a remarkable uniformity of songs, often over thousands of kilometers.

The exact means by which some songbirds are held to a limited set of sounds remains unclear. Marler et al. (1981) argue eloquently that in some way the perceptual development of these birds may be "canalized" (sensu Waddington 1957), just as morphological systems in the body are canalized in their development. The limited set of elements from which Swamp Sparrow songs are constructed is certainly consistent with the idea of "an innate repertoire of note types, with a species-specific morphology that is genetically controlled" (Marler and Pickert 1984:686).

A number of questions remain unanswered. Are sound repertoires of most species really far more restricted than we had formerly appreciated? Is each male singer equipped with some mechanism that identifies rather precisely the appropriate sounds in the environment that must be imitated (cf. Marler 1976)? Is it possible that nonsinging females of many species may actually limit the variability in male songs by responding only to selected sounds that males are capable of producing (King and West 1983)? Clearly, we must reassess how we view song learning in oscines and must

attempt a better understanding of the developmental guidelines and the interplay between genetic and environmental (i.e., learned) factors that control vocal ontogeny (Güttinger 1979, Marler et al. 1981).

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SONG IN THE WHITE-EYED VIREO

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ABSTRACT.—This is an audiospectrographic study of the primary song of the White-eyed Vireo (*Vireo griseus*) based on 16,612 recorded songs of 379 birds from 20 states, Bermuda, and the Bahamas, and representing the five subspecies that occur in the United States. Information is given on song construction, song variation, individual repertoires, singing behavior, song and note type sharing by two or more birds, and geographic variation. The largest song-type repertoire was 17, and most birds had a repertoire of 10 to 14 song types. In most birds represented by a sizeable number of songs, even in well studied areas, a few of the individual's song types were unique (found in no other bird studied), and the rest were shared by other birds; this sharing was with more birds outside the area than in it, with one or more song types occurring in birds several hundred kilometers away. The 614 song types found were classified in five major groups; the incidence of the types in these groups, as well as the song length and the number of notes in the song, varied geographically.
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The songs of a White-eyed Vireo (*Vireo griseus*) are short, and they generally begin and end with a short sharp note; the other notes of the song may be buzzy or musical, and are usually slurred. A common song of this vireo might be paraphrased as "pick-up-the-beeer-check." The songs vary; while different birds, sometimes many kilometers apart, may sing a given song type, songs of different birds are often different.

This paper examines variations in songs of birds from different parts of the United States. I am concerned here solely with primary song (termed "discrete" song by Bradley 1980, 1981), although I have examined recordings containing calls, rambling song, chatter, and sub-song.

Bradley (1981), studying song variation in a local population, based his conclusions on similarities in the notes or elements of the songs. My study is similar, but is based on song types as well as individual notes, and is based on more birds, from different parts of the country.

METHODS AND MATERIALS

I have examined 463 recordings of White-eyed Vireo song, believed to represent 379 birds (see Tables 1 and 2). Most of these recordings were made by me and are housed in the tape collection of the Borror Laboratory of Bioacoustics, Ohio State University, but I have been provided with copies of recordings from the following people and institutions: Richard A. Bradley (48 recordings), Cornell Laboratory of Ornithology (36 recordings), Florida State Museum (12 recordings), Sam Houston State University (10 recordings), and North Carolina State Museum (6 recordings).

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TABLE 1

DATA ON SONG AND NOTE TYPE UNIQUENESS

Area or subspecies[a]	No. of birds	No. of songs	Song types: Total found[b]	Song types: Found in only 1 bird: No.	Song types: Found in only 1 bird: %	Note types: Total found[b]	Note types: Found in only 1 bird: No.	Note types: Found in only 1 bird: %
Ohio areas								
Cast	10	332	28	8	29	63	0	0
DWA	6	176	19	7	37	54	1	2
Hb	8	1345	46	17	35	74	1	1
BW	14	1633	49	20	41	84	3	4
DCP	12	443	42	22	52	75	1	1
CCV	35	1100	46	8	17	80	0	0
ZSF	35	3822	80	27	34	88	4	5
BOSP	10	986	40	11	28	65	1	2
SSF	29	1817	65	19	29	90	2	2
Total	159	11,654	221[b]	139	63	135[b]	13	10
All Ohio	186	12,021	235	154	66	142	13	9
novaboracensis	211	12,368	267	183	69	166	19	11
griseus	124	3371	267	206	77	264	51	19
maynardi	26	519	50	46	92	147	30	20
bermudianus	1	21	6	6	100	23	4	17
micrus	17	327	31	29	94	91	14	15
All birds[c]	379	16,612	614	470	77	375	118	32

[a] Abbreviations for the Ohio areas are explained in the text.
[b] Number of different types.
[c] Seven song types were found in two subspecies. Three note types, AA (the final note in song 7) (Fig. 1), CC (the first note in song 4) (Fig. 1), and PC (the first note in song 21) (Fig. 2), were found in all five subspecies, 35 were found in four subspecies, and many were found in two or three subspecies.

To obtain as much as possible of each bird's song-type repertoire, I recorded for 1–2 min (if the bird changed song type during this time I continued recording for another 1–2 min), then stopped and waited until the bird changed songs before continuing the recording. If a bird stopped singing I played back to it some songs of this species; this usually started the bird singing again. On subsequent visits to the bird's territory, if the bird was not singing when I arrived, I used playbacks to start it singing.

The playbacks used in the field were of three types: one (song 46, Fig. 3) a type found in only one bird studied, another (song 1, Fig. 1) found in 29 birds, and the third (song 2, Fig. 1) found in 41 birds. The three types proved equally effective in inducing singing, and the songs sung by the birds involved differed on different occasions.

I made sonagrams of each song type in each recording with a Sona-Graph 7029A, using the wide band setting. Time and frequency scales were obtained from the Sona-Graph, and note and song lengths were measured on the graphs to the nearest 0.01 sec. Individual birds were assigned numbers.

Many localities are represented in the material studied, but the following Ohio areas, where much of my recording was done, are referred to by abbreviations: BOSP—Burr Oak State Park, Morgan County (6 seasons); BW—Blendon Woods Metro Park, Franklin County

TABLE 2

DATA ON SONG LENGTH AND NOTE CONTENT

Subspecies	Location	No. of birds	No. of songs	Song length (sec)[a]		No. of notes in song[a]	
				Range	Mean[b]	Range	Mean[b]
novaboracensis	CT, NY, NJ, PA, OH, IN, IL, NB,	195	12,116	0.24–2.42	1.13 ± 0.003	1–17	8.19 ± 0.02
	WV, KY, TN, NC, AL	16	252	0.40–1.58	1.08 ± 0.02	2–14	8.21 ± 0.14
	Total	211	12,368	0.24–2.42	1.13 ± 0.003	1–17	8.19 ± 0.02
griseus	MD, VA, NC, SC, GA	22	356	0.44–1.83	0.97 ± 0.01	2–16	7.44 ± 0.11
	Gainesville, FL	46	1799	0.42–2.30	1.05 ± 0.005	2–17	7.40 ± 0.05
	FL Panhandle	41	892	0.60–2.11	1.05 ± 0.01	3–15	7.30 ± 0.06
	LA, central TX	15	324	0.63–1.79	1.15 ± 0.02	4–18	9.16 ± 0.15
	Total	124	3371	0.42–2.30	1.05 ± 0.004	2–18	7.55 ± 0.04
maynardi	South FL, Bahama	26	519	0.58–1.38	0.94 ± 0.01	3–13	6.49 ± 0.08
bermudianus	Bermuda	1	27	0.90–1.73	1.17 ± 0.03	4–8	6.70 ± 0.21
micrus	South TX	17	327	0.65–1.38	0.90 ± 0.01	4–13	7.19 ± 0.21
All birds		379	16,612	0.24–2.42	1.10 ± 0.002	1–18	7.98 ± 0.02

[a] Based on all songs studied.
[b] $\bar{x} \pm$ SE.

(12 seasons); Cast—Resthaven Wildlife Area, Castalia (8 seasons); CCV—Clear Creek Valley and vicinity, Hocking and Fairfield Counties (20 seasons); DCP—Darby Creek Metro Park, Franklin County (10 seasons); DWA—Delaware Wildlife Area, Delaware County (5 seasons); Hb—Highbanks Metro Park, Delaware County (4 seasons); SSF—Shawnee State Forest, Scioto County (12 seasons); and ZSF—Zaleski State Forest, Vinton County (10 seasons).

The term "note" is used in this paper for an individual unit of sound, and is represented on a sonagram by a continuous mark, or by two or more marks that overlap in time; the term "song type" is used for a particular sequency of notes making up a song; other terms in the literature for song type are motif or theme (Baptista 1976), song pattern (Marler and Isaac 1961), or simply "song" (Thorpe 1961).

Anyone attempting to recognize note or song types in a bird's vocalizations always faces the problem of how different notes or songs must be to be considered different types, or how much notes or songs may differ and still be recognized as the same type. Any criteria one may use will always be subjective, and different people designating types in the same vocalizations might recognize different numbers of types. No matter what criteria one uses, he will always encounter situations where he has a problem deciding where to draw the line between different types, and any conclusions drawn regarding these types may have to be weighed against the validity of the type designations. In the case of note types, in my study of Bradley's Gainesville, Florida, birds I recognized 149 different note types, whereas Bradley recognized 150, which would suggest that perhaps my note-type designations are reasonably valid.

RESULTS

Song Construction

The notes in a White-eyed Vireo song range in length from less than 0.01 sec to 0.70 sec ($\bar{x} = 0.095 \pm 0.001$ sec [SE]), in frequency from about 1.6 to 8.5 kHz, and in quality from pure tones to harsh or buzzy notes with a pitch range of an octave or more. Most notes are slurred, some over an octave or more in one or two hundredths of a sec. The modulation rate in most buzzes is under 150/sec, but in some may be as high as 350/sec. Most songs begin and end with a short, abruptly slurred note (usually slurred over an octave or more), but there is no definite sequency of the other notes in the song. Some songs contain a rapid series of similar notes, often of decreasing pitch, giving the effect of a short trill or sputter; such a series may be anywhere in the song. About half the notes are ≤ 0.05 sec; about half of the birds studied had long notes (≥ 0.3 sec) in their repertoire, but only 5% of the notes in the songs studied were this long (Table 3). Occasionally a note may be uttered two or more times in succession, or may appear in different parts of the same song.

Each bird's repertoire of note types is used to produce a variety of song types; a given note or note sequence may be used in different parts of different song types. The 45 birds that were represented by over 100 songs each had repertoires of 28 to 54 ($\bar{x} = 42.9$) note types. There was a significant positive correlation in these 45 birds ($r = 0.7413$, $P < 0.001$) between the number of song types and the number of note types. A given

TABLE 3

SONG LENGTH IN THE WHITE-EYED VIREO

Subspecies	Location	No. of notes studied[a]	Note length (sec)	% of the note types of different duration (sec)			% of birds with long notes[c]	% of notes that were long[c]
				≤0.05	0.051–0.10	>0.10		
novaboracensis	CT, NY, NJ, PA, OH, IN, IL, NB,	4206	0.10 ± 0.002	50.9	14.4	34.8	62.6	5.9
	WV, KY, TN, NC, AL	190	0.08 ± 0.006	55.3	18.4	26.3	50.0	4.7
	Total	4396	0.10 ± 0.002	51.0	14.6	34.4	61.6	5.8
griseus	MD, VA, NC, SC, GA	241	0.09 ± 0.006	44.8	24.1	31.1	27.3	2.9
	Gainesville, FL	985	0.10 ± 0.003	43.8	19.0	31.2	54.3	3.7
	FL Panhandle	545	0.09 ± 0.004	43.5	26.6	29.9	43.9	5.0
	LA, central TX	229	0.08 ± 0.005	54.1	21.8	24.0	20.0	1.3
	Total	2000	0.09 ± 0.002	45.0	22.0	33.0	41.9	3.7
maynardi	South FL, Bahama	306	0.91 ± 0.005	43.5	25.5	31.0	41.9	3.7
bermudianus	Bermuda	24	0.11 ± 0.017	33.3	33.3	33.3	0	0
micrus	South TX	182	0.08 ± 0.006	52.2	22.0	25.8	29.4	2.7
All birds		6908	0.10 ± 0.001	48.9	17.5	33.6	51.5	5.0

[a] The totals of the number of note types for each bird studied.
[b] $\bar{x} \pm$ SE.
[c] Long notes = >0.3 sec; the number of birds studied in the different areas is given in Table 2.

note in these 45 birds was used in 1–11 ($\bar{x}$ = 2.0) different song types, and 31.3–73.0% ($\bar{x}$ = 46.1%) of the note types were used in only one song type. The number of notes in the songs varied from 1 to 18 (Table 2).

Song Types

The different utterances of a given song type by a given bird were usually almost identical. There were a number of cases in the songs studied where a song type (of an individual bird) was represented by two or more variations—usually in where, along a particular sequence of notes, the song ended, or in the number of times a note was repeated (where note repetition occurred). Only rarely was there variation in how the song began (in songs of a given sequence of notes).

I recognized 614 song types in the songs studied, and in classifying these I used as the primary basis the least variable part of the songs, the beginning. Two songs were considered to be different types if they began differently, or if they contained different note types. As with note types, one will always encounter problems in deciding where to draw the line between different song types, especially when dealing with songs of different birds, but I believe my song-type designations are reasonable. Some of the figures (e.g., songs 30–32, Fig. 3) illustrate what I consider to be the same song type sung by different birds.

I arranged the song types of this vireo, based on how the songs began, in five major groups:

Group 1.—Songs beginning with 2 to 6 short notes of decreasing pitch, these notes somewhat similar to the call of a Summer Tanager (*Piranga rubra*) (songs 1, 19, 22, 30, 31, 32; cf. 43–45) (Figs. 1–3).

Group 2.—Songs beginning with two or more repetitions of a particular note (songs 15, 20) (Fig. 2).

Group 3.—Songs beginning with a hoarse or buzzy note, this note short and containing frequencies ranging over an octave or more (songs 12, 21, 25) (Figs. 1, 2).

Group 4.—Songs beginning with a short, sharp, musical note, this note abruptly slurred over an octave or more (songs 2–3, 5–11, 13–14, 16–18, 23–24, 33–40) (Figs. 1–3).

Group 5.—Songs beginning with a long note, this note either buzzy or musical, and its frequencies ranging over less than an octave (songs 4, 41, 42) (Figs. 1, 3).

Each of these five major groups was further subdivided, with a total of 59 subgroups; each subgroup was designated by one or two letters, and the types in each subgroup were numbered. Each song type was designated by a number-letter-number combination; e.g., type 4bc–13 (song 14, Fig. 2) was the thirteenth type in major group *4*, subgroup *b*, sub-subgroup *c*.

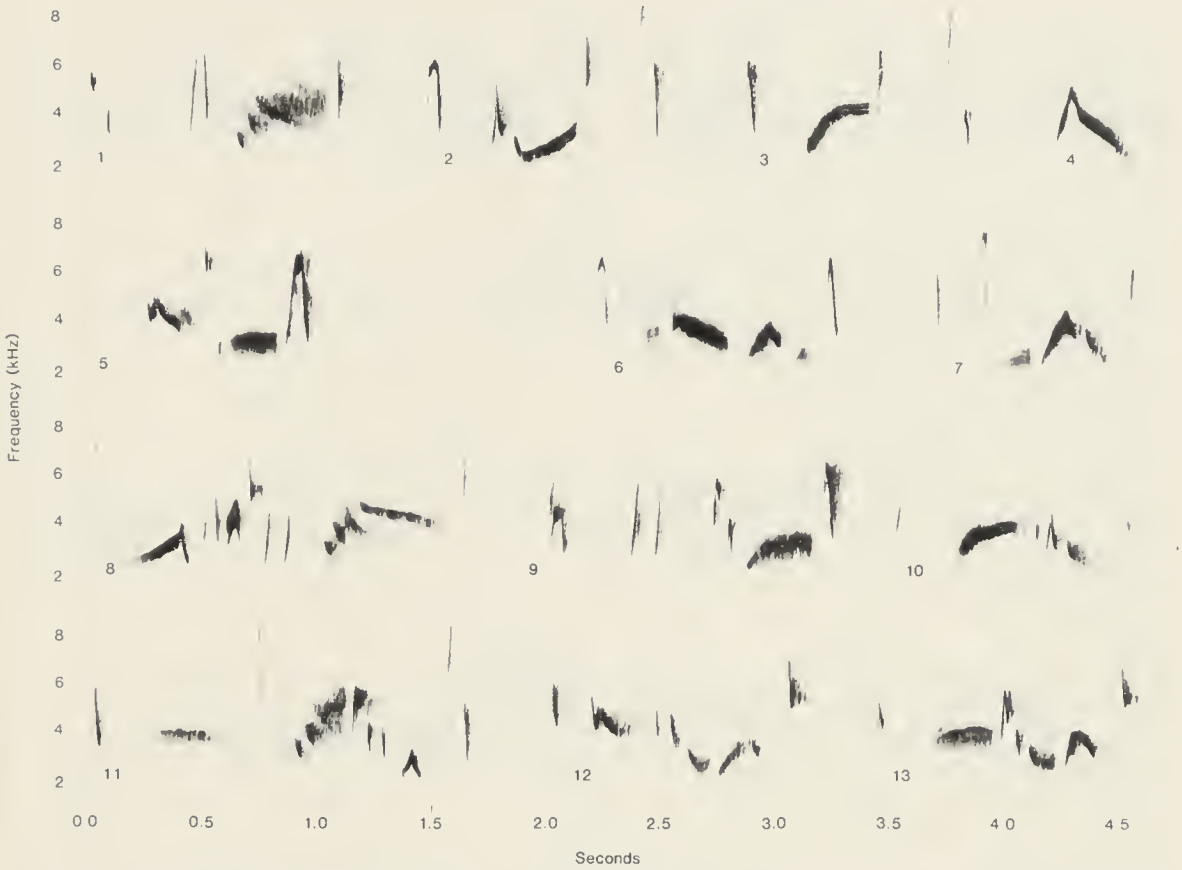

FIG. 1. Sonagrams of the 13 song types of White-eyed Vireo No. 101, Zaleski State Forest, Vinton County, Ohio, June 1980. The numbers in parentheses (in this and the other figure captions) are the number of the recording, and the song in the recording, from which the sonagram was made. Song 1.—Type 1a-9 (15558-13); found in 29 birds, Ohio and southwestern Kentucky. Song 2.—Type 4e-22 (15558-27); found in 41 birds, Ohio, Indiana, and West Virginia. Song 3.—Type 4bc-10 (15558-31); found in 21 birds, Ohio (Lake Erie to the Ohio River). Song 4.—Type 5aa-1 (15558-42); found only in this bird. Song 5.—Type 4c-26 (15558-32); found in 37 birds, Ohio and eastern Indiana. Song 6.—Type 4bd-4 (15558-36); found in 41 birds, Ohio (Lake Erie to the Ohio River). Song 7.—Type 4fc-7 (15558-54); found in 26 birds, Ohio (Lake Erie to the Ohio River). Song 8.—Type 4bf-8 (15558-53); found in 50 birds, Ohio and West Virginia. Song 9.—Type 4fe-2 (15558-56); found only in this bird. Song 10.—Type 4bc-13 (15560-3); found in 24 birds, central and southern Ohio. Song 11.—Type 4hb-11 (15560-47); found in 30 birds, Ohio and Jackson County, Illinois. Song 12.—Type 3ae-5 (15560-60); found in 41 birds, Ohio, Kentucky, and West Virginia. Song 13.—Type 4hc-7 (15569-2); found in 19 birds, central and southern Ohio.

This classification greatly facilitated determining whether a newly recorded song type had been recorded before. This classification is artificial; I have no evidence that song types in a particular group are used in particular situations.

A White-eyed Vireo sometimes utters single short notes (like the first note of their Group 4 song types) between songs; these were not counted

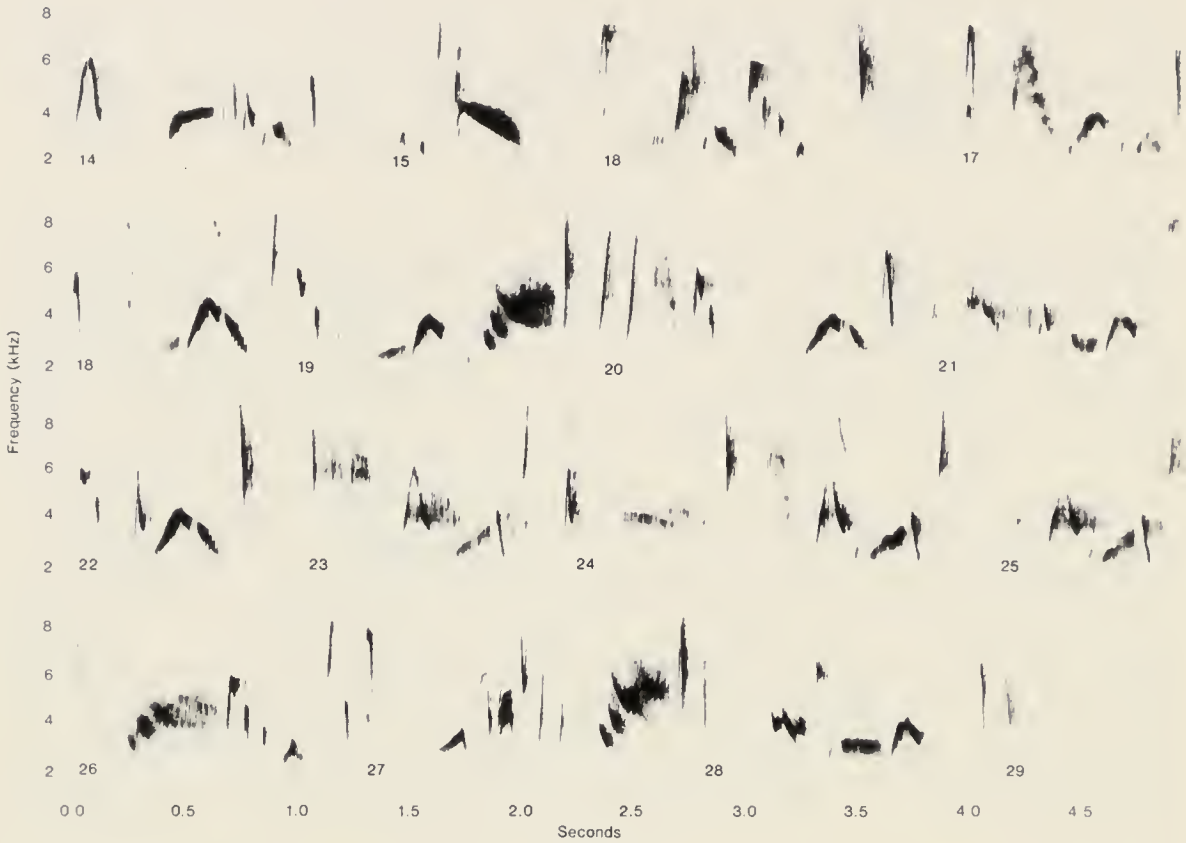

FIG. 2. Sonagrams of the song types of White-eyed Vireo No. 102, Zaleski State Forest, Vinton County, Ohio, June 1980. This bird's territory was about 400 m from that of bird No. 101. Song 14.—Type 4bc-13 (15570-14); see song 10. Song 15.—Type 2a-1 (15570-17); found only in this bird. Song 16.—Type 4e-23 (15575-2); found in 46 birds, central and southern Ohio. Song 17.—Type 4g-2 (15570-2); found in 11 birds, central and southern Ohio. Song 18.—Type 4fc-7 (15564-28); see song 7. Song 19.—Type 1b-4 (15564-44); found in 4 birds, (2 CCV, 2 ZSF). Song 20.—Type 2b-10 (15573-3); found in 6 birds, central and southern Ohio. Song 21.—Type 3ae-5 (15573-11); see song 12. Song 22.—Type 1g-4 (15573-23); found in 24 birds, 22 in Ohio, 1 in Chincoteague, Virginia, and 1 in southwestern Kentucky (Land Between the Lakes). Song 23.—Type 4g-10 (15575-5); found in this bird, another in ZSF, and a bird in BOSP. Song 24.—Type 4hb-6 (15575-21); found in this bird and a bird in Franklin County, Ohio. Song 25.—Type 3af-7 (15575-30); found only in this bird. Song 26.—Type 4hc-3 (15575-13); found in 6 birds, central and southern Ohio. Song 27.—Type 4bf-8 (15577-17); see song 8. Song 28.—Type 4c-25 (15581-1); found in 6 birds, central and southern Ohio. Song 29.—Type 4ha-1 (15575-27); found in 28 birds, 27 in Ohio and 1 in Wakulla County, Florida.

as songs. One bird (from Hb) uttered a note a little like the *wheep* note of a Great Crested Flycatcher (*Myiarchus crinitus*) (like the second note in song 8) (Fig. 1) about a second before some songs of two different types; these were not counted as songs.

The only instance I found of a 1-note song was in bird No. 101 (song 4) (Fig. 1). This was sung in series, like the bird's other song types, and appeared in three of the seven recordings I made of this bird (it appeared

FIG. 3. Sonagrams of White-eyed Vireo songs (songs 30–42 and 46) and Summer Tanager calls (43–45). Song 30.—Type 1g-4 (14863-95), bird 125, SSF (see also song 22). Song 31.—Type 1g-4 (13523-2), bird 141, Land Between the Lakes, Kentucky. Song 32.—Type 1g-4 (14769-2), bird 147, Chincoteague, Virginia. Song 33.—Type 4hc-7 (15144-119), bird 27, BW (see also song 13). Song 34.—Type 4bc-1 (4434-4), bird 176, Tallahassee, Florida. Song 35.—Type 4bc-1 (N. C. St. Mus., 2-6), bird 151, Raleigh, North Carolina. Song 36.—Type 4hb-3 (14054-2), bird 210, Wakulla County, Florida. Song 37.—Type 4hc-7 (14863-11), bird 125, SSF. Song 38.—Type 4hb-3 (15890-6), bird 318, Hb. Song 39.—Type 4hc-7 (14054-8), bird 210, Wakulla County, Florida. Song 40.—Type 4hc-7 (15062-69), bird 126, SSF. Song 41.—Type 5ab-7 (1640B-15), bird 260, Bradenton, Florida. Song 42.—Type 5b-7 (11938-2), bird 208, Wakulla County, Florida. Call 43.—Summer Tanager (4141-2), CCV. Call 44.—Summer Tanager (15566-2), ZSF. Call 45.—Summer Tanager (15566-3), ZSF. Song 46.—Type 4be-2 (12979-2), bird 43, DCP; found only in this bird.

in two parts of one recording). This is unlike any other song or note of this species that I have ever heard or recorded.

Two-note songs (e.g., songs 34, 35) (Fig. 3) were found on 36 occasions, and involved 21 different song types. In 32 of these occasions the 2-note songs appeared to be short versions of a longer song, but in the other 4 occasions (involving two song types, 4bc-1, songs 34–35 of Fig. 3, and 5aa-2) did not.

Song types in Group 4 were the most common, comprising over half (54.7%) of the types found, and an even larger percentage (63.9%) of the

songs studied; over three-fourths of the birds studied (307, or 81%) had one or more song types in this group. Types in Groups 2 and 5 were the least common, comprising only 11.2% of the types found, and an even smaller percentage (5.4%) of the songs studied. On the average, the birds studied used their types in Groups 1–3 in proportion to the number of types they had, but used types in Group 4 more, and types in Group 5 less. Only five of the 379 birds studied (1.3%) had song types in each of the five groups.

Song-Type Repertoires in Individual Birds

A White-eyed Vireo usually sings songs of one type for a while, then changes to another. In the 46 recordings I made containing 100 or more songs, the birds changed song types, on the average, every 3.66 min, but this varied from 1.0 to 9.3 min. If these birds sang at the rate of 12.62 songs/min (the average found; see below), the birds would sing from about 13 to 118 (average, 46) songs before changing to another type. (Barlow [1981] says that this species sings 50–100 songs of one type before changing to another.) If one recorded consecutive songs from a bird singing like this, he would need to record several hundred, perhaps over a thousand, songs before he could be reasonably sure he had all or most of the bird's repertoire. On the other hand, if he recorded like I did—recording a minute or so and then turning the recorder off until the bird changed songs—he would not need as many recorded songs to determine the bird's repertoire.

Fifty-five of the birds studied were represented by over 100 songs; their average repertoire was 11.7 song types and 15.3 variations. In general, for these birds, the more songs studied, the more song types were found. This correlation was significant ($r = 0.60$, $t = 4.96$, $P < 0.001$) for the 55 birds, but for the 15 birds represented by over 200 songs the correlation between the number of songs studied and the song types found was not significant ($r = 0.4483$, $t = 1.8081$, $P > 0.05$). The 29 birds represented by over 150 songs averaged 12.6 song types, the 15 with over 200 songs averaged 13.7 song types, the 11 with over 250 songs averaged 13.4 song types, and the 5 birds with over 300 songs averaged 14.8 song types.

The above analysis suggests that, using the recording techniques that I used, it would be desirable to have a sample of 200 or more songs to get all or most of a bird's repertoire. As the 15 birds in this study that were represented by over 200 songs had an average of 13.7 song types and 18.3 variations, these figures may be a reasonable estimate of an average vocal repertoire for individuals of this species. (Barlow [1981] gives 10–15 as the song-type repertoire size in this vireo.) Some individuals may have as many as 17 song types, and some may have as few as 10 (bird No. 343, ZSF, represented by 253 songs, had only 10 song types).

A Bird's Use of Its Song Types

Passerines with a repertoire of two or more song types use their repertoire in different ways. Some, including the Song Sparrow (*Melospiza melodia*) (Borror 1965), Carolina Wren (*Thryothorus ludovicianus*) (Borror 1956), Rufous-sided Towhee (*Pipilo erythrophthalmus*) (Borror 1975), Cardinal (*Cardinalis cardinalis*) (Lemon 1967), and others, usually sing songs of one type for a while and then change to another; a few, such as the Red-eyed Vireo (*Vireo olivaceus*) (Borror 1981) and Wood Thrush (*Hylocichla mustelina*) (Borror and Reese 1956), sing their songs in a varied sequence, rarely if ever singing the same song type two times in succession. The White-eyed Vireo is a passerine of the first type (i.e., it generally sings songs of one type for a while, then changes to another); when it changes song types, it may do so abruptly, or it may alternate song types for a few songs.

A few passerines sing songs of two types more or less alternately. This occurs in some species that have only two or three song types, such as certain flycatchers (Borror 1967), and it occurs occasionally in species with larger repertoires. It has been reported in the Song Sparrow (Borror 1965) and the Rufous-sided Towhee (Borror 1975), and it occurs occasionally in the White-eyed Vireo. In the case of the vireo, the song types used in alternate-type singing may be the same or different on different occasions, and the song types involved may also be sung in series by themselves. I do not know what significance, if any, song type alternation has in this vireo.

In a few of the wood warblers (Emberizidae, Parulinae), each bird has a repertoire of two song types, one of which is used primarily as an advertising song and the other chiefly in aggressive situations (Borror and Gunn 1985); this is the case in the Black-throated Green Warbler (*Dendroica virens*), the Golden-cheeked Warbler (*D. chrysoparia*), Townsend's Warbler (*D. townsendi*), and probably others. I have no evidence that the different song types of a White-eyed Vireo are used in different situations; a bird may respond to a given playback with different songs on different occasions.

Fifty-four of the 379 birds studied were recorded two or more times: 37 were recorded twice, 13 three times, 2 seven times, and 1 each eight and nine times. In most of these birds the sequence with which the birds' song types were sung differed in the different recordings; the exceptions involved short recordings with only two or three song types. There were no recordings with fewer than 100 songs that contained a particular song type early in the recording and again later in the recording. In the 46 recordings that contained over 100 songs, there were 16 in which one (5 recordings), two (6 recordings), three (2 recordings), four (2 recordings),

or five (1 recording) song types appeared in two different parts of the recording; the second series of a song type came from one-half hour to about two hours after the first series.

It appears then, that in a given bout of singing, a bird will go through most of its song repertoire before repeating a song type, and this repetition may come from one-half to two hours after the first utterance of that song type. The different song types in a bird's repertoire are generally not sung in the same sequence on different occasions.

Playbacks of White-eyed Vireo songs were used in obtaining most of the longer recordings I made. Only one type (type 4be-2, song 46, Fig. 3, which was found in only one bird studied) was used prior to 1982. In 1982 two types were used, 4be-2 and 4e-22 (song 2) (Fig. 1), the latter a type found in 41 birds. In 1983 two types were used, 4be-2 and 1e-9 (song 1, Fig. 1, found in 29 birds). In 1984 and 1985 only type 4be-2 was used. The playbacks nearly always induced the bird to sing. No bird with which 4be-2 songs were used ever responded with songs of that type. Birds with which 4e-22 and 1e-9 songs were used responded with a variety of song types, but only rarely with the same type as the playback. Apparently this vireo only rarely responds to a playback with songs of the same type as the playback, and then only if it has that song type in its repertoire.

Singing rates were calculated from data on the average interval from the beginning of one song to the beginning of the next (termed "cadence" by Reynard 1963), in 63 birds (recorded in 1982, 1983, and 1984, with 6979 intervals). These rates varied from 4.4 to 23.7 songs/min, and averaged 12.62 ± 0.04 songs/min (Reynard 1963 gives the average cadence of 23 White-eyed Vireos as 5.1 sec, which is equivalent to 11.8 songs/min). In 47 birds there were some series preceded by playbacks, and others without playbacks; in 23 of these 47 birds the singing rate was significantly higher following playbacks, in 7 birds it was significantly lower in series preceded by playbacks, and in the other 17 birds the difference in singing rate with and without playbacks was not significant. Overall in these birds, the rate following playbacks ($\bar{x}$ = 13.06 ± 0.05 songs/min) was significantly higher than without playbacks ($\bar{x}$ = 12.25 ± 0.05 songs/min) ($P < 0.05$). In my studies of Song Sparrows in Maine (Borror 1965), I found a somewhat greater increase in singing rate following playbacks, from about 5 to 8 songs/min.

Song Similarities in Different Birds

One may judge the similarities in the songs of different birds by the amount of sharing of song types or note types. Bradley's study of song variation in a Florida population of White-eyed Vireos (1981) was concerned with notes rather than song types. Each note type he found (some-

times note groups) was assigned a 2-letter designation, and each song was designated by a series of these 2-letter terms. Using computer analysis, he obtained values representing the differences between two or more songs or song repertoires. My studies of song similarities in different birds differed from those of Bradley in that I was concerned with the amount of song and note type sharing in different birds. I recognized 614 song types and 375 note types in the songs I studied, which would indicate that there is more variation and less sharing in song types than in note types.

Song type sharing.—Of the 614 song types found, 470 (76.5%) were found in only one bird. The birds studied admittedly represent a relatively small sample of the species population, and come from widely separated localities, but even in areas where considerable recording was done there were a great many unshared song types (Table 1). In one Ohio area (ZSF), where over 3800 songs were recorded from 35 birds, about a third of the song types found were found in only one bird, while in the eight other relatively well studied Ohio areas the proportion of song types found in only one bird ranged from about 17% (CCV) to >50% (DCP) of the song types found. In the case of the different subspecies, the more recording done, the fewer unshared song types were found.

The number of birds in an area having one or more song types shared with other birds was highest where the most recording was done. Of the 379 birds involved in this study, 273 (72.0%) had at least one song type shared with other birds, but in Ohio 183 of the 186 birds studied (98.4%) had at least one song type shared with other birds. This percentage differed in the five subspecies, and may reflect the degree of isolation of the birds involved: *novaboracensis,* 91.9%; *griseus,* 57.3%; *maynardi,* 23.1%; *micrus,* 11.8%; and *bermudianus,* 0.0% (song types found in the one individual of this subspecies studied were found only in this bird).

About two-fifths (59) of the 144 shared song types were shared by only two birds, but 15 types were shared by from 19 to 50 birds. A few song types in this species are found in many individuals, but most are found in only one or a few individuals.

Information on the relation between distance apart and the amount of song type sharing was obtained from two sets of data: (1) the sharings of the song types of the 36 Ohio birds that had ten or more song types, and (2) the sharings of the song types of all the birds recorded in the nine most studied Ohio areas. As these two studies showed essentially the same thing, only the latter is reported here.

For each song type found in each of these nine areas, counts were made of the numbers of birds, at various distances, that shared the type; these numbers were added to produce a set of totals for each area, and the area totals were added to produce a grand total for the nine areas. The figures

for the different areas differed somewhat, due at least in part to the different numbers of birds studied in the different kilometers-away zones. Studies of the sharings of the song types of 36 Ohio birds produced sharing totals that were very similar for the birds in a given area, but differed in different areas. Adding the area totals produces figures that represent an average of all nine areas. Over half of the song-type sharings in these birds occurred in birds over 80 km away (58.3% in Zones 4 and 5, 81–320 km away), while less than one-tenth (9.1%) occurred in birds in the same area (Zone 1). Beyond 320 km (Zones 6 and 7) the sharings dropped off considerably, but there was at least some sharing by birds over 800 km away.

Some of the differences in the percentage figures in Table 4 may be due to differences in the numbers of birds studied in the different distance-away zones; to take this into account, calculations were made of the number of sharings per bird studied in each distance-away zone. These figures are given in the *s/b* lines in Table 4. For all nine areas (bottom line of Table 4) these figures are similar for Zones 1–5, but a little higher in Zone 4, and a little lower in Zones 3 and 5, and considerably lower for Zones 6 and 7.

The data on song type sharing in this vireo suggest that in a bird with 13 or 14 song types (near an average for this vireo), one might expect two or three of these song types to be unique (found only in that bird), and the rest shared with other birds. Of the shared types, one would expect two or three to be shared with other birds in the same area, and the rest shared with birds outside the area. In the case of a bird's song types that were shared by birds outside its area, one would expect that at distances up to 320 km away, about one bird in five would share one or more of its song types, but beyond 320 km the sharings would drop off considerably. Of the sharings found, one would expect most to be with birds 80–320 km away, and at least one would be with a bird over 800 km away.

The higher percentage of shared song types in well studied areas than in more separated areas (e.g., 37.1% for the nine Ohio areas represented in Tables 1 and 4, and 23.5% for all birds studied) may reflect the degree of isolation of many of the birds studied. Large samples in well-studied areas contain fewer unique song types than small samples from widely separated areas. There is little evidence of distinct local dialects in this vireo, but song similarities are greater in populations less than 320 km apart than in more widely separated populations.

The song-type sharings by birds over 800 km apart involved seven different song types: (1) Type 1g-4: found in 22 Ohio birds, a bird in Chincoteague, Virginia, and a bird in southwestern Kentucky (songs 22, 30, 31, 32) (Fig. 2, 3). (2) Type 3c-6: found in 6 Ohio birds and a bird in

TABLE 4

SHARING OF THE SONG TYPES IN NINE OHIO AREAS

Area[a]	No. of birds	No. of shared song types[b]	Item[c]	Distance-away zones[d] 1	2	3	4	5	6	7	Total sharings
Cast	10	20	%	2	<1	—	10	71	17	<1	449
			s/b	0.8	1.0	—	3.1	2.4	1.4	0.01	
DWA	6	12	%	2	17	4	61	16	1	—	258
			s/b	0.8	2.0	0.5	1.4	1.2	0.1	—	
Hb	8	31	%	4	13	20	44	19	1	1	558
			s/b	2.8	2.7	1.8	3.9	3.0	0.2	0.02	
BW	14	29	%	6	19	13	38	23	1	<1	541
			s/b	2.3	2.3	1.8	4.3	2.7	0.2	0.01	
DCP	12	20	%	3	15	22	36	23	1	1	396
			s/b	1.1	1.8	1.9	2.6	2.0	0.1	0.01	
CCV	35	38	%	10	11	53	20	5	1	<1	568
			s/b	1.7	2.4	3.8	3.2	1.9	0.2	0.01	
ZSF	35	53	%	26	9	17	42	5	1	1	630
			s/b	4.7	4.2	2.1	3.4	2.1	0.1	0.02	
BOSP	10	29	%	5	44	4	42	5	1	<1	536
			s/b	2.5	3.3	1.2	2.8	1.9	0.1	0.01	
SSF	29	46	%	14	—	1	58	23	5	1	602
			s/b	2.9	—	1.0	3.3	3.2	0.6	0.02	
Total	159	278	%	9	14	16	38	20	3	<1	4538
			s/b	2.6	2.6	2.2	3.0	2.4	0.4	0.01	

[a] Abbreviations for the Ohio areas are explained in the text.
[b] The number of song types for which counts of sharings were made.
[c] Percent of the total sharings of the song types in the area found in the zone, and the number of sharings per bird (*s/b*) studied in the zone.
[d] Zone 1, the same area (<16 km away); Zone 2, 16–48 km away; Zone 3, 49–80 km away; Zone 4, 81–160 km away; Zone 5, 161–320 km away; Zone 6, 321–800 km away; Zone 7, >800 km away.

Wakulla County, Florida. (3) Type 4bc-1: found in 3 birds—in Raleigh, North Carolina, Leon County, Florida, and Gainesville, Florida. (4) Type 4e-20: found in 5 birds, 4 in Wakulla County, Florida, and 1 in eastern Maryland (Willards). (5) Type 4ha-1: found in 29 Ohio birds and a bird in Wakulla County, Florida (song 29) (Fig. 2). (6) Type 4hb-3: found in a Central Ohio bird, a bird in Northampton County, North Carolina, and a bird in Wakulla County, Florida. (7) Type 4hc-7: found in 18 Ohio birds and a bird in Wakulla County, Florida (songs 37, 39, 40) (Fig. 3).

Two of these seven song types (4bc-1 and 4ha-1) might possibly be considered short versions of a longer type. Type 4bc-1 contains only two notes (songs 34, 35) (Fig. 3), like the first two notes in several other song types. Type 4ha-1 contains three notes (song 29) (Fig. 2), and several song

types begin with these three notes. The Florida bird that sang 4ha-1 songs sang only one song of this type, plus two longer songs beginning with these same three notes; in the Ohio birds with this song type it was sometimes sung more or less alternately with a longer song beginning with these same three notes, and sometimes in a series by itself.

The other five song types sung by birds over 800 km apart were longer songs (see songs 33, 37, 39, 40, and 36, 38) (Fig. 3), and any differences in length (e.g., songs 36 and 38) were minor and of a type encountered in many individual birds.

Note type sharing.—There were many fewer note types than song types in the birds studied (375 note types, compared with 614 song types), and much more sharing of note types than of song types. Of the 375 note types found, 118 (31.5% were found in only one bird; 76.5% of the song types were found in only one bird), and the shared note types were found in from 2 to 225 birds (shared song types in 2 to 50 birds).

Most of the note types that were found in only one bird were found in more or less isolated areas; there were relatively few unshared note types in the songs of birds in well studied areas. For example, of the 80 note types found in CCV birds, none was found in only one bird, and in the SSF birds, where 90 note types were found, only two types were found in a single bird studied (Table 1).

Information on the relation between distance apart and the amount of note type sharing was obtained in the same way as for song types. The total percentage figures for the sharings of note types in nine Ohio areas (comparable to the % line at the bottom of Table 4) were as follows: Zone 1, 6.5%; Zone 2, 9.9%; Zone 3, 11.2%; Zone 4, 26.9%; Zone 5, 15.9%; Zone 6, 6.3%; and Zone 7, 23.2%. The corresponding *s/b* figures for the seven zones (comparable to the last line in Table 4) were: Zone 1, 19.4; Zone 2, 19.9; Zone 3, 17.2; Zone 4, 21.9; Zone 5, 20.0; Zone 6, 10.1; Zone 7, 7.7. The figures on sharing of note types are similar to those for song types, but with a smaller percentage of the sharings in the nearer zones and more in the distant zones. The *s/b* figures on note type sharings are very similar to those for song type sharings: very similar in Zones 1–5, with a noticeable drop in Zones 6 and 7.

Geographic Variation

Five subspecies of the White-eyed Vireo occur in the continental United States and neighboring islands: *V. g. novaboracensis, V. g. griseus, V. g. maynardi, V. g. bermudianus,* and *V. g. micrus. V. g. novaboracensis* occurs throughout the northern part of the species' range, east to the coastal plain areas of Virginia, the Carolinas, and Georgia, and South to about the middle of the Gulf states; *griseus* occurs from central Texas

eastward through the southern portions of the Gulf states, northern Florida, and up the east coast; *maynardi* occurs in peninsular Florida, from Tampa Bay south, and in the Bahamas; *bermudianus* occurs in Bermuda; and *micrus* occurs in southern Texas.

The recordings I studied come from a large section of the species' range in the United States and represent all five subspecies, but the numbers of birds and songs from many areas are probably too small to give an adequate picture of the songs in those areas (Tables 2 and 3).

The data in Table 2 show a tendency toward a decrease in song length and the number of notes in the song going from north to south, but the songs of *griseus* in central Texas averaged longer and contained more notes than songs from most other areas. There was little variation in the average note length in songs from different parts of the country (Table 3), but the notes of Texas birds (*griseus* in part, and *micrus*) averaged shorter than those in songs elsewhere. In general, the proportion of a bird's notes that were very short ($\leq$0.05 sec), decreased going from north to south, but short notes were more common in Texas birds than in most others. The relative number of birds with long notes in their repertoire ($\geq$0.3 sec) tended to decrease going from north to south, and was lowest in Texas birds and in the *griseus* from the southeastern states. On the average, 5.0% of the notes of the birds studied were long notes ($\geq$0.3 sec); this percentage was highest in *novaboracensis,* and lowest in Texas and Bermuda birds.

The incidence of song types in the five major groups differed somewhat in different parts of the country. Songs of types in Group 1 were more common in most of the South than in the North, and types in Group 4 were less common. Songs of types in Group 3 were more common in the deep South (southern Florida and southern Texas) than elsewhere. Song types in Group 2 were moderately common in the Southeast, but were less common in the South than in the North. Song types in Group 5 occurred more often in the southern states than elsewhere.

V. griseus is divided into subspecies on the basis of differences in color; I would not divide it into subspecies on the basis of song.

DISCUSSION

My findings agree fairly well with those of Bradley (1980, 1981), though we approached song variation somewhat differently. Bradley (1981: 82) gave the average song length as 1.02 sec (N = 213), while the songs I studied (N = 16,612) averaged 1.10 sec in length (1.05 sec for 1799 songs from Gainesville; Bradley apparently based his figures on the song types found, rather than on all the songs he studied). We both found that a bird responding to playbacks does not attempt to match the song type of the

playback. His finding of a lack of correlation between the song (element) similarity and distance apart in a local area agrees with my findings (for song and note types) over a larger area.

None of the birds I recorded was color banded or otherwise marked for individual identification, but most of my recordings (and probably all of the Ohio recordings) were made during the nesting season—and recordings made in a given territory during the same season were assumed to be of the same bird. Conversely, recordings made in different territories were assumed to be of different birds. As no two birds studied had the same song-type repertoires, this repertoire may also serve as a means of individual identification. Birds whose territories are close together may share a few song types, but only a few. Birds 101 and 102, which were recorded the same week in June, 1980, about 400 m apart, shared four song types: songs 7 and 18, 8 and 27, 10 and 14, and 12 and 21 (Fig. 1, 2); their other song types were different.

Although a human observer may learn to recognize individual White-eyed Vireos by their song-type repertoire, I do not know whether or not individual vireos can do this. There is much experimental evidence (Falls 1982) indicating that many birds can recognize other individual birds by their songs (or at least distinguish between neighbors and strangers); this ability appears more pronounced in species in which each individual has only one song type; as repertoire size increases, this ability appears to decrease (Falls 1982). It has been suggested that in birds with a sizeable song type repertoire a bird may sing its most distinctive songs more frequently, but this does not appear to be the case in the White-eyed Vireo. (This point was checked in 36 Ohio birds that had one or more unique song types, and were represented by either 100 or more songs or had 10 or more song types. In these 36 birds, on the average, 20.8% of their song types, but only 18.8% of their songs, were unique; these birds averaged 16.3 songs per type of their unique types, and 17.3 per type of their shared types.) My playbacks of White-eye songs to White-eyes in the field were designed to increase their singing, not to determine the bird's ability to distinguish between different songs.

Most of my recordings of White-eyed Vireos were made in a few areas, over a period of several years. I have frequently recorded a bird in the same place in successive years, but I have only once found a bird that I thought was the same bird I had recorded there the previous year. Bird 329 was recorded in the same area in 1982 and 1983 (in BW); 13 of its 17 song types were sung both years. This bird sang 14 song types in 1982 (1 not sung in 1983), and 16 types in 1983 (3 not sung in 1982). I believe the fact that 13 song types were sung in this area both years indicates that

the same bird was there both years. Seven of the 17 song types sung by this bird were not found in any other bird studied.

Song variation in this vireo is much like that in the Song Sparrow (i.e., each bird has a repertoire of several song types, and sings one for a while and then changes to another). In my study of Song Sparrows in Maine (Borror 1965), I found very little song type sharing by different birds (but considerable note type sharing), but I did find a number of instances of individual birds (identified by their song type repertoires) returning to approximately the same territory in successive years.

Studies of banded birds have shown that many birds return to a given nesting area in successive years. Barlow (pers. comm.) found Gray Vireos (*V. vicinior*) returning to breeding areas in western Texas as many as four years in a row, and he found Black-capped Vireos (*V. atricapilla*) returning in successive years to breeding territories in Texas and Oklahoma. I have no information on recoveries of banded White-eyed Vireos returning to the same breeding areas in successive years, but Rappole and Warner (1980) report banded White-eyed Vireos returning to the same wintering area in Mexico in successive years.

There are three possible reasons why I did not find more instances of White-eyed Vireos returning to the same breeding area in successive years: (1) they seldom return to the same territory because of a high over-winter mortality; (2) they return to a different territory; or (3) they may return to the same territory, but have changed song types and I do not recognize them. The first possibility seems unlikely, as I see no reason why White-eyed Vireos should have higher over-winter mortality than do Song Sparrows, Gray Vireos, or any of the other species in which returning to the same territory in successive years has been shown by banding. Barlow (pers. comm.) reports instances of banded Gray Vireos returning to the same territory, in which they sang different song types in successive years. As my birds were not banded, I have no way of checking this possibility in my birds, but because of my experience with other species, I doubt that a White-eyed Vireo would change its song types from one year to the next.

Two intriguing questions arise with this vireo—as well as in many other passerines: (1) just how does a bird come to sing the particular song types that it sings, and (2) how can one explain the geographic distribution of song types that he finds. In many species, including this vireo (Bradley 1981) there is evidence that some songs, or some features of the songs, are learned from males in the area where the bird was reared. If this is a significant method of song acquisition in the White-eyed Vireo, we would expect to find (in a nonmigratory population, or in one returning to the

same area in successive years) the song similarities greater the closer together the birds were. This does not appear to be the case in the White-eyed Vireo, either from my study or that of Bradley (1981). (Bradley was dealing with a nonmigratory population, while most of my birds were form migratory populations.)

The songs of a White-eyed Vireo (and of other species as well; see Borror 1981) are very variable before the types become fixed—as though the birds were experimenting with different note types and sequences—and the particular song types that become fixed and in the primary song repertoire may be to some extent a matter of chance, with perhaps in some species a tendency for the bird not to duplicate too closely the songs of its neighbors.

The higher percentage of the song type sharings in Zone 4 (81–160 km away) (Table 4) appears to be due to the larger numbers of birds studied in that zone. Figures on the number of sharings *per bird studied* (*s/b* figures in Table 4) show only a slight increase in the sharing in Zone 4. The *s/b* figures in Table 4 show a similar amount of song type sharing up to a distance of 320 km.

Attempts have been made to explain the geographic distribution of song types of birds (see Lemon et al. 1985), but most of the factors suggested do not appear to have been important in the case of the White-eyed Vireo, principally because each male of this vireo has a repertoire of song types that differs in character and distribution (see Fig. 1, 2). It is probable that the distribution of White-eyed Vireo song types reflects only the effects of chance, with no direct selection involved (as suggested by Slater et al. 1980 for the Chaffinch [*Fringilla coelebs*]). The "chance" factor in this vireo has probably been affected by the mechanism of song acquistion (through the influence of neighboring males in the area where the bird was reared) and the apparently uncommon return of a bird to the same area in successive years.

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CAVITY-TREE SELECTION BY RED-COCKADED WOODPECKERS AS RELATED TO GROWTH DYNAMICS OF SOUTHERN PINES

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Abstract.—We compared measurements at 212 Red-cockaded Woodpecker (*Picoides borealis*) cavity trees and 150 randomly selected mature pines in eastern Texas. Discriminant analyses indicated that cavity trees were significantly older and taller, with greater crown depths, volumes, and weights, and larger diameters at breast height than were randomly selected mature pines. Examination of growth increment cores indicated that cavity trees had undergone a period of suppressed growth after which they were released by some type of natural or man-caused thinning. Because shelterwood cutting imitates the suppression and release phenomenon we observed, we suggest that this harvest technique be used instead of clearcutting in areas around woodpecker colonies in order to provide an immediate and sustained supply of potential cavity trees. *Received 30 Sept. 1986, accepted 22 Jan. 1987.*

Red-cockaded Woodpecker (*Picoides borealis*) colonies in eastern Texas have decreased in number over the past 30 years (D. W. Lay, pers. comm.). Declines and extirpation of active colonies also continue elsewhere (Thompson 1976; Baker 1983; M. A. Byrd, pers. comm.; J. A. Jackson, pers. comm.; R. F. Labisky, pers. comm.). The recovery of endangered species should include a demonstrated population increase. Because the Red-cockaded Woodpecker is a cooperative breeder, a true recovery must include an increase in the number of breeding units (clans or colonies). The fact that we are not observing the formation of new colonies by pioneering or budding (Hooper 1983) throughout the Red-cockaded Woodpecker's range suggests that our management may be inadequate and that alternative management techniques may be needed, particularly for populations (demes) where fewer than 250 colonies exist (see Franklin 1980).

Most studies on Red-cockaded Woodpeckers have focused on descriptions of nesting habitat (Lay and Russell 1970, Ligon 1970, Morse 1972, Grimes 1977), foraging habitat (Ligon 1968, Morse 1972, Skorupa and McFarlane 1976, Nesbitt et al. 1978, Hooper and Lennartz 1981), and home-range size (Baker 1971, Skorupa and McFarlane 1976, Hooper et al. 1982, Nesbitt et al. 1982). A few studies have examined specific characteristics of pine trees, such as age, presence of heartwood decay, and

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growth form, that are important to the species and perhaps serve as search images for cavity-tree selection (Thompson 1971, Jackson 1977b, Jackson et al. 1979, Conner and Locke 1982, Locke et al. 1983). Recently, Field and Williams (1985) have suggested that the importance of age is questionable.

Because Red-cockaded woodpeckers nest in live cavity trees that actively ooze oleoresins at resin wells, the amount of resin a cavity tree can produce may also be an important characteristic for the woodpeckers. Classic studies in naval stores (turpentine industry) indicate that crown characteristics and vigor of pines are related to the production of oleoresins (Wahlenberg 1946). Growth history of cavity trees may also be important to cavity-tree selection because it can affect tree appearance and wood structure.

We examined differences among 212 Red-cockaded Woodpecker cavity trees and 150 randomly selected mature pines. Our objectives were to (1) determine if Red-cockaded Woodpeckers selected specific pine trees for cavity excavation and (2) identify any special characteristics of the cavity trees that may relate to stand management techniques necessary to grow such trees.

STUDY AREA

The Angelina National Forest (Angelina, Jasper, Nacogdoches, and San Augustine Counties) includes 62,423 ha of forested lands in eastern Texas. Approximately 49% of this forest is northeast of Sam Rayburn Reservoir, and 51% is southwest. Red-cockaded Woodpeckers in the northeast portion of the Angelina National Forest are found in stands comprised mainly of loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines. Those to the southwest are primarily in longleaf (*P. palustris*) pine forests. Active colonies northeast of the reservoir are a minimum of 34 km from active colonies to the southwest.

METHODS

We searched for, located, and tagged 212 Red-cockaded cavity trees during 1983 and 1984. Two people examined each tree in mid-April (the beginning of the nesting season) and concurred on whether the tree was active or not. We judged resin wells to be active if the bark bordering the well was red (indicating recent pecking [Jackson 1978a]), and clear, fresh resin was flowing from the well. Cavity trees without any active resin wells were considered inactive (Jackson 1977a). We examined cavity trees closely from all sides to ensure that fresh resin or reddish bark around wells was not the result of Pilcated Woodpecker (*Dryocopus pileatus*) activity (early stages of cavity enlargement and foraging sites, which are common), Cerambycid beetle oviposit sites, Yellow-bellied Sapsucker (*Sphyrapicus varius*) feeding sites, or injury.

A noncavity tree was selected by walking a varying predetermined distance into stands and using a board-game spinner device to indicate the tree to be selected. If an obviously young tree was indicated, the spinner was spun again. Four or 5 of the most mature noncavity-tree pines were selected within 37 stands of mature pine forest for comparisions with cavity trees. We selected the 37 most mature forest stands available using National Forests of

Texas continuous inventory of stand conditions (CISC) data for the Angelina National Forest. To reflect the relative proportions of cavity-tree species, 26 of the 37 stands were longleaf pine and 11 loblolly and shortleaf pine. All stands where we randomly selected mature pines were at least 150 m from Red-cockaded Woodpecker cavity trees, but still within areas potentially frequented by woodpeckers during foraging activities.

We measured characteristics of 212 cavity trees (during the summer of 1984) and 150 randomly selected trees (spring 1985), as well as the habitat immediately surrounding them (Table 1). We extracted 5 mm-diameter increment cores from pines at breast height and used a binocular dissecting scope to count annual growth rings. Three years were added to the number of increments for loblolly and shortleaf pines and 5 years to longleaf pines to determine the age of trees from the time they germinated (L. C. Walker, pers. comm.). We were unable to age 22 of the cavity trees because the heartwood at breast height was decayed. Each core was examined for signs of suppression or stress as indicated by tightly packed growth rings; it was judged that suppression had occurred if there was a growth rate of ≥ 16 growth rings/cm for a period of 5 years or longer. We noted the total number of contiguous years that each tree was suppressed, as well as the age of the tree if and when a release (as indicated by sudden return to large growth increments) occurred. The percentage of years that each tree had been growing under suppressed conditions was calculated. The number of growth increments in the outer 2 cm of each pine's sapwood was measured to evaluate recent growth trends.

We determined crown shape (conical, parabolic, cylindrical), measured the drip line, and estimated what portion of the crown was present (for asymmetrical crowns), and from these values we calculated a crown volume for each tree. Crown weights (branch wood, branch bark, needles) were calculated from tree height and diameter at breast height (DBH) measurements (see Taras and Clark 1975, 1977; Clark and Taras 1976). Crown depth was measured as the vertical distance between the top of the crown and the lowest major branches on the bole of the tree. Tree and midstory height were measured with a clinometer. Bole length was determined by subtracting crown depth from tree height. Bark thickness (cm) was measured at breast height. Basal areas were measured with a 1-factor metric prism, using each cavity tree or randomly selected pine as the center of the sampling point.

We used a 2-tailed t-test to compare characteristics of cavity trees with those of the randomly selected mature pines (random pines). Discriminant function analysis (DFA) was used to evaluate differences between cavity trees and random pines. Correlations of original variables to the discriminant axes were used to evaluate the importance of variables to the discrimination (Bargmann 1970, Timm 1975).

RESULTS

Red-cockaded Woodpecker cavity trees differed from randomly selected mature pines on the Angelina National Forest (Table 1). Regardless of whether tree species were combined or examined separately, Red-cockaded Woodpecker cavity trees were older and taller, with greater crown depths, volumes, and weights, larger diameters at breast height, and slower recent growth than were random pines. Within tree species groups, bark thickness of cavity trees was greater than that of the random pines (Table 1).

Because many tree characteristics, especially the crown and tree size, are usually correlated with tree age, some differences we detected between

TABLE 1

COMPARISONS OF VARIABLE MEANS MEASURED AT AND AROUND RED-COCKADED WOODPECKER CAVITY TREES AND RANDOMLY SELECTED MATURE PINES IN THE ANGELINA NATIONAL FOREST IN EASTERN TEXAS

Variables	Longleaf pines		Loblolly and shortleaf pines		All pine species	
	Cavity trees (N = 151)	Random pines (N = 97)	Cavity trees (N = 61)	Random pines (N = 53)	Cavity trees (N = 212)	Random pines (N = 150)
Tree						
Age (year)[a]	126.4	56.7[b]	86.9	61.2[b]	114.5	58.3[b]
Crown depth (m)	9.5	6.1[b]	9.0	7.0[b]	9.4	6.4[b]
Crown volume (m^3)	405.7	129.7[b]	419.6	221.0[b]	409.7	162.7[b]
Crown weight (kg)	450.5	237.7[b]	555.8	328.8[b]	480.8	271.2[b]
Diameter at breast height (cm)	47.5	36.3[b]	52.7	41.5[b]	49.0	38.2[b]
Tree height (m)	24.2	22.9[c]	28.1	26.0[b]	25.4	24.0[d]
Bole length (m)	14.7	16.8[b]	19.1	18.9[e]	16.0	17.6[b]
Bark thickness (cm)	1.9	1.8[f]	2.3	1.9[d]	2.1	1.8[d]
No. growth increments in last 2 cm	17.1	12.7[b]	13.6	11.5[f]	16.1	12.3[b]
Stand						
Total basal area (m^2/ha)	15.8	19.6[b]	16.3	23.9[b]	15.9	21.2[b]
Basal area of pine overstory (m^2/ha)	14.1	17.2[b]	13.7	16.9[b]	14.0	17.1[b]
Basal area of pine midstory (m^2/ha)	1.1	1.6[e]	1.1	2.2[c]	1.1	1.8[c]
Basal area of hardwood overstory (m^2/ha)	0.2	0.1[f]	0.3	0.3[e]	0.2	0.2[e]
Basal area of hardwood midstory (m^2/ha)	0.4	0.8[f]	1.1	4.5[b]	0.6	2.1[b]
Midstory height (m)	2.9	5.1[b]	5.6	8.1[c]	3.7	6.2[b]

[a] See Table 2 for sample size—some cavity trees were decayed in center.
[b] t-test, $P < 0.0001$.
[c] t-test, $P < 0.01$.
[d] t-test, $P < 0.001$.
[e] Not significantly different, $P > 0.05$.
[f] t-test, $P < 0.05$.

cavity trees and the random pines could have been related to cavity tree age. Our comparision of cavity trees and random trees of similar ages (the subset of 80–100 year-old longleaf pines was the only age and species group with sufficient sample size; there were 87 degrees of freedom) indicated that crown depth (t-test, $P < 0.0001$), crown volume ($P < 0.001$), crown weight ($P < 0.001$), and diameter at breast height ($P < 0.001$) were greater for cavity trees than random pines. Average age of the cavity trees

in this subset of trees was 97-years-old, and random trees averaged 91-years-old ($P < 0.05$). Thus, even in this subset, tree age was significantly different although to a much lesser degree than crown measurements. We detected no significant differences in tree height and bark thickness between 80 and 100-year-old cavity and random longleaf pines.

Stands immediately surrounding cavity trees had lower total basal area and basal area of pine overstory trees than stands around the random pines (Table 1). Within tree species groups, areas around cavity trees had lower hardwood midstory basal area and midstory height than areas around random pines.

Examination of increment cores showed that longleaf pine cavity trees had a longer average period of suppression, longer percentage of life suppressed, and older age at time of release than random longleaf pines (Table 2). More than 77% of longleaf pine cavity trees showed marked signs of suppression and release, whereas only 23.5% of random longleaf pines exhibited signs of suppression and release. When it was observed in the random trees, the transition between suppressed increments and released increments was much less obvious than in the cavity trees. Although suppression and release occurred in 56% of loblolly and shortleaf pine cavity trees and only 46% of random loblolly and shortleaf pines, we detected no significant differences in the duration of suppression, percentage of life suppressed, and age at time of release between cavity and random trees (Table 2). When all tree species were combined, results followed the same significance pattern observed for longleaf pines separately.

Most cavity trees germinated 40 years prior to the extensive wave of timber harvesting that swept through eastern Texas and peaked around 1910 (Maxwell and Baker 1983) (Fig. 1A). Whereas a sustained and gradual release of suppressed pines apparently occurred prior to 1890, the extensive harvesting from 1890 to 1930 may have provided the release for most of the cavity trees in existence on the Angelina National Forest today (Fig. 1B). The skewed nature of the distribution of cavity tree age (Fig. 1C) may reflect the removal of many existing older cavity trees by the surge of timber harvesting that occurred around the turn of the century. Most of the random pines on the Angelina National Forest germinated after the major timber harvests of the early 1900s (Fig. 1C). Relative to tree age, active cavity trees were a subset of all cavity trees (Fig. 1C and D). The youngest active cavity tree (64-years-old) germinated about 1921, whereas the youngest inactive cavity tree (45-years-old) germinated around 1940. The oldest active cavity tree (205-years-old) germinated in 1780, while the oldest inactive cavity tree (328-years-old) germinated in 1657.

Examination of cores from cavity trees indicated that they had grown

TABLE 2

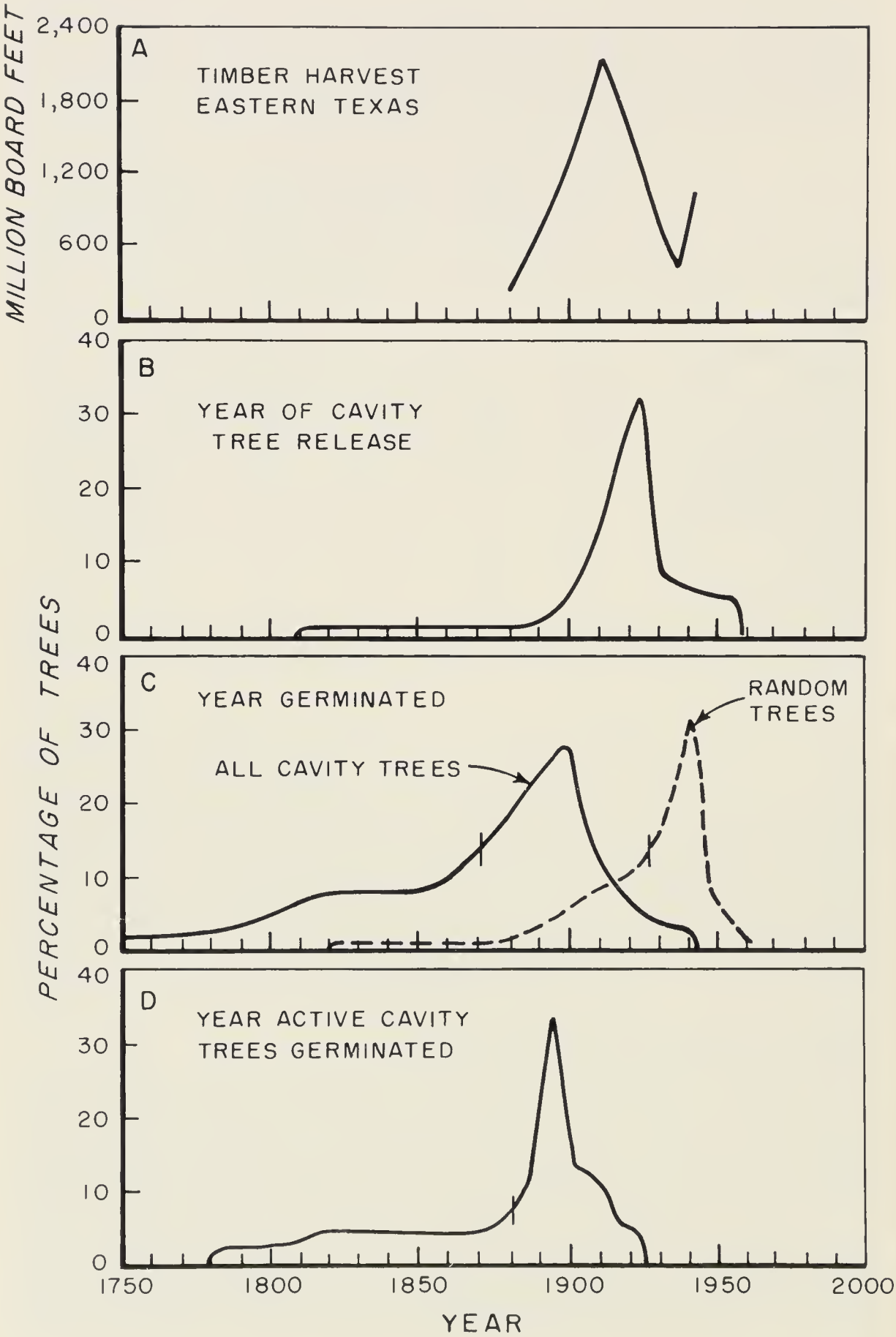
COMPARISONS OF VARIABLE MEANS MEASURED FROM INCREMENT CORES EXTRACTED AT BREAST HEIGHT FROM RED-COCKADED WOODPECKER CAVITY TREES AND RANDOMLY SELECTED MATURE PINES ON THE ANGELINA NATIONAL FOREST IN EASTERN TEXAS

Variables	Longleaf pines		Loblolly and shortleaf pines		All pine species	
	Cavity trees (N = 133)	Random pines (N = 97)	Cavity trees (N = 57)	Random pines (N = 52)	Cavity trees (N = 190)	Random pines (N = 150)
Age (years)	126.4	56.7[b]	86.9	61.2[b]	114.5	58.3[b]
Duration of suppression (years)	48.2	6.7[b]	9.6	7.8[e]	36.6	7.1[b]
Percent of life suppressed	31.4	7.3[b]	10.5	11.4[e]	25.1	8.7[b]
Year germinated	1857	1928[b]	1898	1924[b]	1870	1926[b]
Year released	1919	1949[b]	1926	1948[b]	1921	1949[b]
Age of release (years)	72.2	40.7[d]	31.2	29.0[e]	62.5	34.7[b]
Number of trees showing suppression and release	103	23	32	24	135	47
Percent of trees showing suppression and release	77.4	23.5	56.1	46.2	71.1	31.3

[b,d,e] See footnotes in Table 1.

under two general conditions. Most of the older cavity trees (120–328 years old, N = 65) had probably begun their initial growth within an older forest stand. They were suppressed from the day they germinated—one had been suppressed for 200 years. Eventually these trees were released by some type of natural or human-caused thinning of overstory trees. The released trees began to grow vigorously, filled out their crowns somewhat, and eventually were selected by Red-cockaded Woodpeckers for cavity excavation. The above pattern of growth suggests that these cavity trees may have grown up in an uneven-aged forest or were subdominant in small even-aged stands (Chapman 1909).

Most of the cavity trees younger than 120-years-old were not suppressed when they first germinated. Their initial growth was vigorous as demonstrated by widely spaced growth increments. A gradual decrease in the spacing of rings when the trees were 15–25-years-old indicated that as these trees matured, suppression began with competition for light, moisture, etc. These future cavity trees were subsequently released by some sort of thinning, and vigorous growth ensued. This pattern of growth suggests an even-aged forest stand where pines became suppressed when the canopy closed but were later released by some type of thinning.


MILLION BOARD FEET
2,400
1,800
1,200
600
0
A
TIMBER HARVEST
EASTERN TEXAS
PERCENTAGE OF TREES
40
30
20
10
0
B
YEAR OF CAVITY
TREE RELEASE
C
YEAR GERMINATED
RANDOM
TREES
ALL CAVITY TREES
D
YEAR ACTIVE CAVITY
TREES GERMINATED
1750
1800
1850
1900
1950
2000
YEAR

Discriminant function analyses (contrasting cavity trees with randomly selected mature pines) indicated that tree age, diameter at breast height, and crown characteristics were variables that accounted for the greatest differences between cavity trees and the random pines (Table 3). These characteristics transcended tree species. In general, characteristics of individual trees (such as age, DBH, and crown variables) had greater importance for discrimination between cavity trees and random trees than did stand characteristics (basal area measurements). In all three DFA's, discrimination of cavity trees from random trees was very highly significant, and subsequent classification of trees into the correct group exceeded 90%.

An additional DFA, using only data from tree cores to compare all cavity trees with all random trees (N = 190 and N = 150, respectively; $P < 0.0001$; 87% of cases classified correctly), indicated that tree age ($r = 0.64$, $P < 0.001$), age of release ($r = 0.34$, $P < 0.01$), duration of suppression ($r = 0.33$, $P < 0.01$), and percentage of life suppressed ($r = 0.18$, $P < 0.01$) were significantly correlated to the discriminant axis and were the most important variables discriminating between cavity and random trees.

DISCUSSION

Red-cockaded Woodpeckers used cavity trees that averaged more than 55 years older than the random pines (Table 1). Although Field and Williams (1985) suggest otherwise, age *is* a very important factor for a variety of reasons. Pines younger than 50-years-old typically have very little heartwood; most of the tree is composed of sapwood (Koch 1972). Thus, only older trees usually have enough heartwood to house a cavity. Sapwood probably is unsuitable for cavity excavation because its living cells actively ooze oleoresins. Resins flowing from sapwood could soon render a nest cavity unusable, particularly in healthy pines. Heartwood is composed of only dead plant cells and thus does not actively ooze resin. Also, the older the tree, the wider the heartwood is in higher regions of the tree; thus cavities may be excavated higher in the tree. High nest cavities may be particularly important if resin flow from resin wells is not to be ignited by prescribed or natural fire (Conner and Locke 1979). High cavities may also be more difficult for rat snakes (*Elaphe obsoleta*) to reach than are low cavities. Dennis (1969) observed that the average

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FIG. 1. Timber harvest in eastern Texas (A) shown in relation to year of cavity tree release (B), year in which cavity and random trees germinated (C), and year in which active cavity trees germinated (D).

TABLE 3

RESULTS OF THREE DISCRIMINANT FUNCTION ANALYSES (DFA) CONTRASTING RED-COCKADED WOODPECKER CAVITY TREES WITH RANDOMLY SELECTED MATURE PINES ON THE ANGELINA NATIONAL FOREST IN EASTERN TEXAS

	Longleaf pines	Loblolly and shortleaf pines	All pine species
DFA results			
N for cavity trees	151	61	212
N for random pines	97	53	150
$\bar{x}$ for cavity tree group	1.14	1.24	1.13
$\bar{x}$ for random pine group	−1.17	−1.43	−1.61
Overall DFA significance	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
% of cases correctly classified	92	90	92
Correlation[a] of original variables to the discriminant axis			
Tree age	0.62	0.61	0.58
Diameter at breast height	0.57	0.59	0.54
Crown weight	0.31	0.51	0.39
Crown depth	0.40	0.23	0.38
Crown volume	0.37	0.23	0.36
Total basal area		−0.56	−0.34
Basal area pine overstory		−0.43	−0.22
Tree height		0.27	
Basal area hardwood midstory		−0.24	−0.25
Bark thickness		0.23	

[a] Only correlations with $P < 0.01$ are included.

height of successful nests of Northern Flickers (*Colaptes auratus*) was greater than the average height of unsuccessful nests.

Older trees often have heartwood decaying fungi that decay and soften the heartwood of prospective cavity trees (Steirly 1957, Jackson 1977b, Conner and Locke 1982). Cavities in trees with a decayed heartwood are more easily excavated because the wood tissue is physically easier to chisel out. The extremes of time required to excavate cavities by Red-cockaded Woodpeckers (less than 4 months, R. A. Beck, pers. comm.; 1 year or more, Jackson 1977b) may reflect the time required for excavation of cavities in pines with and without heartwood decay. The incidence of heartwood decay in southern pines is related to tree age and stress (Wahlenberg 1946, 1960). Nelson (1931) reported the frequencies of heartwood decay in various age groups of loblolly pines: 40–90-years-old, 5.4% with heartrot; 91–140-years-old, 18.6%; 141–190-years-old, 60%; 191–230-years-old, 72.2%. Wahlenberg (1946, 1960) considered the frequency of heartwood decaying fungi to be low in loblolly pines less than 75-years-old and longleaf pines less than 100-years-old.

Old pine trees may be important to Red-cockaded Woodpeckers for yet another reason. Resin wells kept active by woodpecker pecking may deter predators such as the gray rat snake (*Elaphe obsoleta spiloides*) (Dennis 1971; Jackson 1974, 1978b). Resin flowing from resin wells eventually loses its gummy quality and hardens, becoming of little use in deterring rat snakes (Jackson 1978b). Old pines have slower resin crystallization rates than do younger pines (Hodges et al. 1977). Thus, resin from resin wells in old pine trees will remain sticky and keep its deterrent quality longer than resin from younger pines.

Cavity trees exhibited the phenomenon of suppression and then release significantly more than did random pines. Although the suppression-release phenomenon could be an artifact of tree age, suppression may also lead to characteristics conducive to cavity excavation that are independent of age. For example, suppression may cause lower limbs to be dropped, cause additional heartwood to form, or make the tree more susceptible to fungal heartrot. Field observations of cavity trees suggest that Red-cockaded Woodpeckers prefer trees with clear boles up to the region of the tree where cavities are excavated (Locke et al. 1983, R. N. Conner, pers. obs.; J. A. Jackson, pers. comm.; D. W. Lay, pers. comm.). The clear tree bole may help prevent rat snakes from climbing cavity trees.

Following suppression and release, precavity trees apparently return to fairly vigorous growth as indicated by greatly increased distances between growth increments. The return to vigorous growth also may be indicated by the significantly larger crowns of cavity trees in contrast to random pines (Table 1). Woodpecker selection of trees with large crowns again may relate to oleoresin production. Bushy, heavy-topped longleaf pines have been observed to yield 40% more resin than do pines with smaller crowns (Wahlenberg 1946). Borrowing from James' (1971) concept of habitat "Gestalt," Red-cockaded Woodpeckers may search for cavity trees with an open bole and a large crown.

Nearly all pines grown in a forest stand will eventually be suppressed unless some type of thinning or cutting occurs. In natural stands, insects, disease, or fire often provide a release for surviving trees to return to more vigorous growth. The sudden release and return to relatively vigorous growth noticed in Red-cockaded Woodpecker cavity trees was not widely observed in the random pines and would not be the typical growth pattern in most short-rotation, even-aged managed forests because such trees are typically clearcut.

During the later stages of the Red-cockaded Woodpecker cavity tree's life, growth again slowed down as indicated by the number of growth increments in the outer 2 cm of sapwood (Table 1). Much of this decrease in growth rate may relate to senescence, but we suspect that additional

growth-retardant stress may be caused by woodpecker excavation and maintenance of resin wells.

We detected that woodpecker cavity trees were in stands with significantly lower basal area and less hardwood midstory than were random pines (see Jackson 1971, Hooper et al. 1980, Lennartz et al. 1983, Hovis and Labisky 1985) (Table 1). A release of the suppressed "precavity" tree may be necessary to create the open, low basal area stands that Red-cockaded Woodpeckers apparently prefer around their cavity trees (Jackson 1971, Hooper et al. 1980, Lennartz et al. 1983, Locke et al. 1983). The DFA's we calculated indicated that cavity tree variables such as age, diameter at breast height, and crown size were more important to the discrimination between cavity and random trees than were stand variables such as basal area and amount of hardwood midstory (Table 3). These observations suggest that individual tree characteristics may be of greater importance in Red-cockaded Woodpecker habitat selection than general forest stand characteristics.

MANAGEMENT IMPLICATIONS

Timber management that results in suppressed tree growth followed by a release from suppression should result in suitable Red-cockaded Woodpecker cavity trees. An existing silvicultural system that might mimic the conditions that apparently produced the trees chosen as cavity trees in eastern Texas today is the shelterwood method. Although a shelterwood reproduction cut harvests most trees, it leaves some selected mature pines standing to provide seeds and shelter for the next generation of pines (Society of American Foresters 1981). This harvesting technique would permit the release of unharvested mature pines from relatively dense, stressed stands to grow with greater vigor, fill out their crowns and provide a prompt supply of potential cavity trees.

A modified shelterwood cut of 80-year-old longleaf pines or a thinning cut to a basal area of about 9 m^2/ha (75 mature pines/ha) offers a harvest management option of potential value to Red-cockaded Woodpeckers. We suggest a pine basal area of 9 m^2/ha because it is the upper limit for a shelterwood cut (Society of American Foresters 1981) and about the lower limit of basal area (9–14 m^2/ha) for quality Red-cockaded Woodpecker habitat (Hooper et al. 1980). Because the current zone suggested for Red-cockaded Woodpecker recruitment stands is between 400 and 1200 m of an active colony (U.S.D.A. 1984), shelterwood or thinning cuts should be used in pine stands that are within 1200 m of active woodpecker colonies for maximum potential recruitment of new colonies. After shelterwood trees have grown to about 120-years-old, their removal could be considered if they have not been colonized by woodpeckers. Leaving

shelterwood trees to provide foraging habitat until they die should also be considered.

Use of shelterwood cuts such as we describe would eliminate the problems encountered when trying to determine where recruitment stands need to be placed. At present, it is often difficult for wildlife managers to find appropriately aged stands at the correct distances from active woodpecker colonies. Shelterwood cut areas would be available for both recruitment of new colonies and for foraging habitat.

Historically and recently, southern pine beetles (*Dendroctonus frontalis* Zimm.) have killed extensive areas of pine forest in the South (Thatcher et al. 1980, Kulhavy and Conner 1986). Pine beetle infestations can kill Red-cockaded Woodpecker cavity trees if colonies are in dense pine stands (Jackson et al. 1986). Shelterwood cuts would greatly reduce timber stand density and, thus, reduce the hazard of beetle infestation in stands around cavity trees.

Red-cockaded Woodpeckers have declined in abundance in the past 30 years (Thompson 1971, Wood 1983). Although recent research suggests that clearcutting may not cause an increase in territory size or immediate declines in nesting success (Wood et al. 1985), the effects of clearcutting are still poorly documented (Thompson 1976). The decline of the woodpecker during a period when clearcutting is the usual management method does not speak well of its effect on Red-cockaded Woodpeckers. Our proposed management strategy and other alternatives should be implemented on an experimental basis. Input from silviculturists is needed to develop a complete management plan that permits a sustained yield of both Red-cockaded Woodpecker habitat and timber. As with any wildlife-timber management practice, its effects should be evaluated prior to widespread implementation.

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AVIAN HABITAT RELATIONSHIPS IN PINYON-JUNIPER WOODLAND

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ABSTRACT.—Habitat relationships of breeding birds were examined in northwestern Colorado in pinyon-juniper (*Pinus edulis-Juniperus osteosperma*) woodland and in openings where most overstory trees had been knocked down by anchor chaining. Vegetation characteristics and physical habitat features were measured in 233 0.04-ha circular plots around singing males of 13 species of birds from 15 May to 15 July 1980. Thirteen-group discriminant function analysis ordinated bird species along three habitat dimensions described by (1) canopy height; (2) slope, shrub size, and shrub species diversity; and (3) percentage canopy cover, large tree density, distance from a habitat edge, litter cover, and green cover. Woodland, open-area, and intermediate edge species were clearly segregated along the first discriminant axis, and species' associations with shrubs, inclination, ground cover, and edges were revealed by the ordinations along the second and third discriminant axes. Two-group discriminant analyses comparing occupied and available plots identified additional and more specific habitat associations. For example, Hermit Thrushes (*Catharus guttatus*) were associated with mature forested habitats and forest interiors, Virginia's Warblers (*Vermivora virginiae*) favored steep, oak-covered draws, Rock Wrens (*Salpinctes obsoletus*) selected areas where percentage log cover and small tree density were high, and Dusky Flycatchers (*Empidonax oberholseri*) preferred shrubby slopes with scattered large trees near woodland edges. *Received 28 Aug. 1986, accepted 15 Jan. 1987.*

Pinyon-juniper woodland is one of the most expansive plant communities in the U.S., occupying some 172,000 km^2 of land (Clary 1975). It dominates much of the landscape in the Southwest, and in New Mexico it occupies 26% of the land surface (Pieper 1977). Because of its relatively low commercial value, vast areas have been converted to grazing lands, especially since 1950, by removing overstory trees. Chaining has been the most widely used conversion technique and involves dragging an 80–200-m anchor chain (20–40 kg/link) between 2 bulldozers, which knocks down the trees (Aro 1975).

Despite the expansiveness and rapid type-conversion of pinyon-juniper woodlands, these areas have been largely ignored by avian ecologists. Balda and Masters (1980) provided an overview of the ecology of the avifauna, and others have examined the effects of type-conversion on breeding birds (O'Meara et al. 1981, Sedgwick and Ryder 1986). Limited information exists, however, on the habitat relationships of songbirds breeding in pinyon-juniper woodlands. This study identifies habitat as-

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sociations of breeding birds in pinyon-juniper woodland, including woodland where most of the trees had been knocked down by chaining.

STUDY AREA

The study was conducted in northwestern Colorado in the Piceance Basin, an area ranging from 1737 to 2590 m in elevation. The dominant overstory vegetation in the area is pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*). Low elevation woodlands on shales are dominated by juniper with an understory of scattered prairie junegrass (*Koleria cristata*), bluebunch wheatgrass (*Agropyron spicatum*), needle-and-thread (*Stipa comata*), bottlebrush squirreltail (*Sitanion hystrix*), Indian ricegrass (*Oryzopsis hymenoides*), and sometimes stunted antelope bitterbrush (*Purshia tridentata*) and true mountainmahogany (*Cercocarpus montanus*). Common forbs include groundsel (*Senecio* spp.), skyrocket gilia (*Gilia aggregata*), penstemon (*Penstemon* spp.), Hood phlox (*Phlox hoodii*), and Nuttall golden weed (*Haplopappus nuttallii*). Pinyon pine, big sagebrush (*Artemisia tridentata*), and western wheatgrass (*A. smithii*) join on sandstone to form a more diverse plant community. Above 2100 m, pinyon pine dominates the overstory, and the shrub layer is composed of big sagebrush, rabbitbrush (*Chrysothamnus* spp.), antelope bitterbrush, and occasionally true mountainmahogany, common chokecherry (*Prunus virginiana*), and Saskatoon serviceberry (*Amelanchier alnifolia*). Gambel oak (*Quercus gambelii*) is prominent on steep slopes and frequently occurs in shady ravines. The grass-forb community above 2100 m includes most species found at lower elevations, but percentage ground cover is higher; arrowleaf balsamroot (*Balsamorhiza sagittata*) and lupine (*Lupinus* spp.) are also frequently present.

I collected data over the entire range of environmental variation in the pinyon-juniper type. This included both undisturbed pinyon-juniper habitat and openings created by chaining. Study sites included (1) xeric, low-elevation stands of nearly pure juniper; (2) shrub-dominated stands with only scattered pines and junipers; (3) mesic, high-elevation stands dominated by pinyon pines; and (4) chainings that varied in age from 4–17 years and in size from 0.2 to 7 km^2.

METHODS

Habitat selection was studied from 15 May to 15 July 1980. Singing males encountered while walking through chained and unchained pinyon-juniper woodland were considered as centers of 0.04-ha circular plots within which vegetation was sampled. Such plots are thought to be representative of the breeding habitat of many species of birds (James 1971, Smith 1977). I used modifications of sampling techniques described by James and Shugart (1970) and Shugart and Patten (1972). Determinations of canopy cover and several categories of ground cover were made while pacing along each of four randomly oriented, orthogonal transects (radii) in each circular plot. By sighting directly upward through an ocular tube on alternate steps, limbs or green vegetation were considered as positive scores for canopy cover. Similarly, presence of bare ground, forb cover, grass cover, shrub cover, litter cover, and log cover were determined by sighting downward through the tube about 1 m in front of the observer. A cover type sighted through the cross hairs of the ocular tube was considered a positive score. Twenty sightings for canopy cover and 20 for

ground cover were made in each circular plot. Using a Biltmore "reach stick" (Forbes 1955), I determined live tree density by counting the number of trees in each of 9 diameter-at-breast-height (dbh) size classes. I used the Bitterlich variable radius technique to determine basal areas of dead, live, and "part" live trees (trees with ≥25% dead limbs) by species (Grosenbaugh 1952). A measure of openness of the habitat was determined by counting the number of quadrants in each circle without trees. The point-centered quarter method (Cottam and Curtis 1956) was used to determine shrub density. I measured canopy height using triangulation techniques (Whitmore 1975) and estimated slope to the nearest five degrees. Slope orientation was derived after the method of Smith (1977). In all, 39 measured and created variables were used in the analysis (Table 1).

Analytical techniques.—Stepwise descriptive discriminant analysis (DDA) (Williams 1983) was used to ordinate bird species along dimensions of habitat and to describe species-species relationships in the context of habitat. DDA attempts to distinguish statistically (discriminate) between two or more groups (species of birds) by forming linear, additive combinations of variables on which the groups are expected to differ (quantitative measures of habitat). A 13-group DDA was performed on a data set which included 13 species of birds (N = 233), each with a sample size ≥10 (Table 2). A stepwise variable entry technique selected the "best set" of habitat variables and reduced the complexity of the original variable set. Discriminant scores were determined for each observation by summing the products of the coefficients and the values of their associated variables. Bird species were ordinated along the discriminant functions according to their mean discriminant scores. Confidence ellipses of species' bivariate means for the first two discriminant functions were computed using the technique of Sokal and Rohlf (1969).

Stepwise 2-group DDA was performed for each of the 13 bird species, comparing sites occupied by each species with the pooled set of sites occupied by all remaining species. I considered the sites occupied by all other species as available habitat. This analysis puts emphasis on individual species-habitat relationships and provides a better resolution of species-specific habitat requirements (Conner et al. 1983). Thirteen separate DDAs were performed, one for each species.

Predictive discriminant analysis (PDA) (Williams 1983) was used to provide an empirical test of the discriminating power of the variables selected by DDA and to provide additional insight into habitat selection and habitat segregation. PDA derives a set of functions (one for each species) that classify observations (habitat information from the circular plots) into groups (bird species). The Statistical Program for the Social

TABLE 1

DESCRIPTIONS OF THE MEASURED AND DERIVED VARIABLES USED IN HABITAT SELECTION ANALYSES, PICEANCE BASIN, 1980

Mnemonic	Description
ALT	Altitude (m)
BITPL	Basal area of live pinyons (using Bitterlich method)
BITJL	Basal area of live junipers
BITOL	Basal area of live oaks
BITLIVE	BITPL + BITJL + BITOL
BITPD	Basal area of dead pinyons
BITJD	Basal area of dead junipers
BITDEAD	BITPD + BITJD
BITPP	Basal area of live pinyons with ≥25% dead limbs
BITJP	Basal area of live junipers with ≥25% dead limbs
BITPART	BITPP + BITJP
BITALL	BITLIVE + BITDEAD + BITPART
BITZERO	Number of quadrants of 0.04-ha circle without trees
CANHT	Canopy height (m)
DENSTYA	Tree density (dbh = 0–15.2 cm)
DENSTYB	Tree density (dbh = 15.2–22.9 cm)
DENSTYC	Tree density (dbh = 22.9–38.1 cm)
DENSTYD	Tree density (dbh = 38.1–53.3 cm)
DENSTYE	Tree density (dbh = 53.3–68.6 cm)
DENSTYF	Tree density (dbh = 68.6–83.8 cm)
DENSTYG	Tree density (dbh = 83.8–101.6 cm)
DENSTYH	Tree density (dbh = 101.6–119.4 cm)
DENSTYI	Tree density (dbh > 119.4 cm)
EDGDIST	Distance (m) to a habitat edge
EWDIREC	East-west slope orientation
GRNDSP	Number of forb and grass species in 0.04-ha circle
NSDIREC	North-south slope orientation
PBARE	Percentage bare ground
PCANOPY	Percentage canopy cover
PCOVER	Percentage ground cover (includes grass, forbs)
PDEADTR	Percentage dead trees (BITDEAD/BITALL)
PGCOVER	Percentage green cover (grass, forbs, and shrubs)
PLITTER	Percentage litter cover
PLOG	Percentage log cover (includes chaining debris)
SHRBHT	Mean shrub height
SHRBDIM	Mean shrub diameter
SHRUBSP	Number of shrub species in 0.04-ha circle
SHRBDEN	Shrub density
SLOPE	Estimate of ground slope (to nearest 5°)

TABLE 2
BIRD SPECIES SEEN ON THE STUDY AREA AND USED IN THE DISCRIMINANT ANALYSES

Mnemonic	N	Species
MD	14	Mourning Dove (*Zenaida macroura*)
DF	11	Dusky Flycatcher (*Empidonax oberholseri*)
RW	18	Rock Wren (*Salpinctes obsoletus*)
HT	10	Hermit Thrush (*Catharus guttatus*)
BGG	20	Blue-gray Gnatcatcher (*Polioptila caerulea*)
SV	13	Solitary Vireo (*Vireo solitarius*)
VW	15	Virginia's Warbler (*Vermivora virginiae*)
BTG	28	Black-throated Gray Warbler (*Dendroica nigrescens*)
GTT	30	Green-tailed Towhee (*Pipilo chlorurus*)
RST	20	Rufous-sided Towhee (*P. erythrophthalmus*)
VS	17	Vesper Sparrow (*Pooecetes gramineus*)
CS	18	Chipping Sparrow (*Spizella passerina*)
BS	19	Brewer's Sparrow (*S. breweri*)

Sciences computer package (SPSS, Version 8) was used for all analyses (Nie et al. 1975).

RESULTS AND DISCUSSION

Thirteen-Group DDA.—Seventeen of the original 39 variables were selected by DDA for discriminating among the 13 species of birds. Three discriminant functions explaining 78.0% of the among-species variance had significant discriminating power ($P < 0.01$) and were ecologically interpretable (Table 3). The first function explained >50% of the among-species variance; canopy height (CANHT), with a coefficient of 0.65, was the dominant variable in discriminant function 1 (DF1). This function may be interpreted as a dimension of trees, representing a continuum from an open, treeless situation to one where large, mature trees are predominant. Bird species occurring in open areas would be expected to have low discriminant scores, and species found in mature pinyon-juniper should have high scores for this function. Discriminant function 2 (DF2) explained an additional 17% of the available discriminating information, and showed a heavy weighting on slope, shrub species richness (SHRBSP), and shrub size (SHRBHT). This function described a gradient from a relatively flat situation, where shrubs were small and shrub species richness was low, to one where shrubs, especially large shrubs on slopes, were predominant. DF3 explained 10% of the discriminating information and contrasted large trees (DENSTYE), percentage canopy cover (PCANOPY), and distance from a habitat edge (EDGDIST) with percentage litter

TABLE 3
SUMMARY OF THE 13-GROUP DISCRIMINANT ANALYSIS

Variable	Discriminant function coefficients[a]		
	Function 1	Function 2	Function 3
CANHT	−0.65	0.08	0.13
PCANOPY	−0.07	−0.32	−0.71
PGCOVER	−0.19	0.36	0.53
PLITTER	−0.21	−0.04	0.50
PBARE	−0.17	0.42	0.34
PDEADTR	−0.11	0.27	−0.15
BITJD	−0.06	−0.07	0.23
DENSTYA	0.23	0.06	−0.15
DENSTYB	−0.23	0.28	0.10
DENSTYE	−0.13	−0.03	−0.53
DENSTYI	0.04	0.22	0.02
SHRUBSP	0.08	−0.64	0.19
SHRUBHT	0.02	−0.45	−0.28
EDGDIST	0.05	−0.37	−0.53
SLOPE	−0.29	−0.62	0.13
ALT	−0.28	0.41	0.27
EWDIREC	−0.19	0.24	0.17
% variance explained[b]	50.4	17.3	10.3
Cumulative % variance explained	50.4	67.7	78.0

[a] Coefficients indicate relative contributions of the variables to each function.
[b] Percentage variance indicates the amount of the among-groups variance accounted for by each function.

(PLITTER) and percentage green cover (PGCOVER). Thus, this function described a gradient going from grassy, shrubby situations to those where a habitat edge was distant, large trees were dominant, and percentage canopy cover was high.

Species associated with open areas versus those from woodland habitats were clearly separated along DF1 (Fig. 1). Hermit Thrush (see Table 2 for scientific names) and Solitary Vireo, for example, which occurred only in mature woodland, lay farthest to the left along DF1, whereas species associated with chainings or natural openings in pinyon-juniper (e.g., Brewer's Sparrow, Rock Wren) were farthest to the right. Chipping Sparrow, often associated with pinyon-juniper edges, was midway along the axis ranging from "openness" to "trees." Virginia's Warbler, Dusky Flycatcher, and Rufous-sided Towhee were often found on steep slopes where shrub cover was high and these species had the lowest scores along DF2. At the opposite end of DF2 were Chipping Sparrow and Vesper Sparrow which occurred in flatter areas where shrubs were smaller and less diverse. Hermit Thrush preferred interior woodlands and had the lowest score

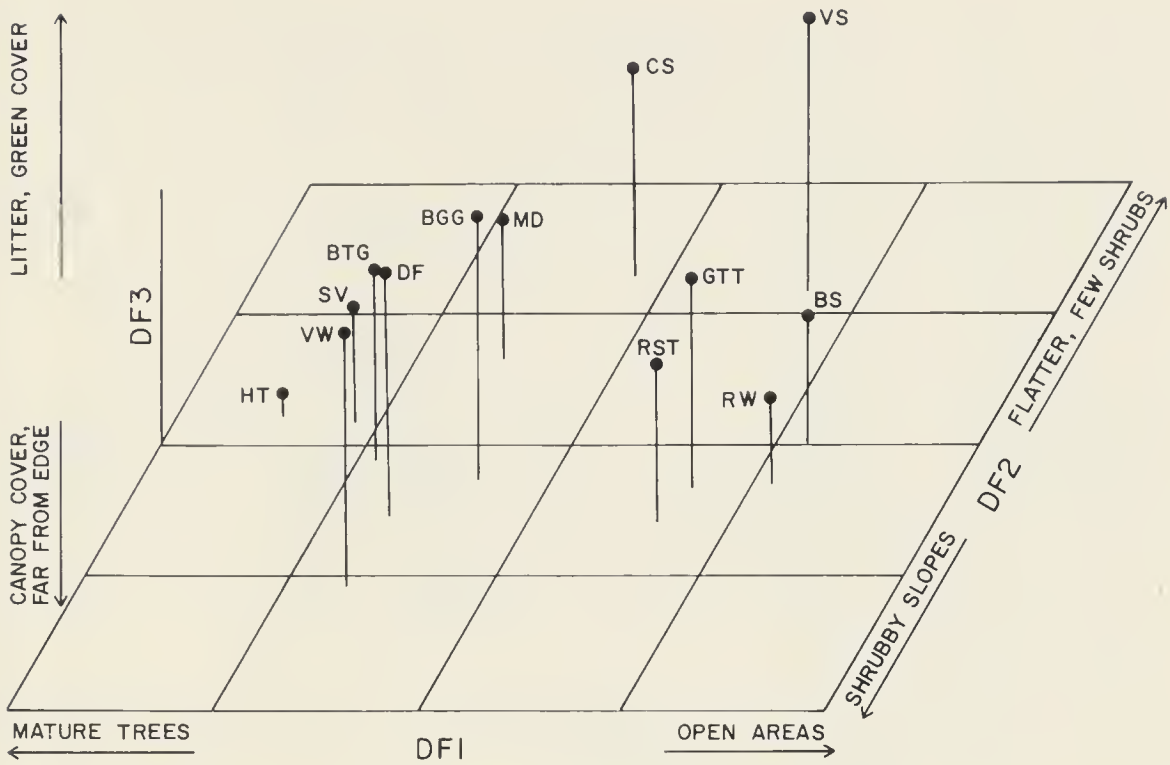

FIG. 1. Ordination of 13 bird species along discriminant axes 1, 2, and 3. See Table 2 for key to species' symbols.

along DF3. Chipping and Vesper sparrows, Virginia's Warbler, Dusky Flycatcher, and Blue-gray Gnatcatcher had the highest scores along this axis, and they preferred high grass, forb, and shrub cover, less canopy cover, or were associated with edges.

Group classification.—PDA correctly assigned 48.9% of the 233 observations to their appropriate groups (Table 4). This is 44.6% better than chance classification (Cohen's Kappa statistic, Wiedemann and Fenster 1978) and is significantly better than could have occurred by random sampling (Z statistic for Kappa, $P < 0.05$). Five species had <50% of their cases correctly classified (Table 4). Three woodland species (Blue-gray Gnatcatcher, Solitary Vireo, and Black-throated Gray Warbler) had positions near the center of the woodland group in discriminant 3-space and overlapped extensively in habitat space with other species (Figs. 1 and 2). Black-throated Gray Warblers were frequently misclassified as Virginia's Warblers, Blue-gray Gnatcatchers, Mourning Doves, or Hermit Thrushes. Blue-gray Gnatcatcher observations were misclassified most as Virginia's Warbler, Mourning Dove, or Black-throated Gray Warbler observations. Solitary Vireos were often misclassified as Hermit Thrushes, Black-throated Gray Warblers, or Blue-gray Gnatcatchers. High misclassification rates for these species suggest a high degree of ecological similarity with the species they were misclassified as regarding the 17 habitat

Table 4

Classification Matrix for 13-group Discriminant Analysis

	Predicted group membership (%)												
Actual group	MD	DF	RW	HT	BGG	SV	VW	BTG	GTT	RST	VS	CS	BS
MD[a]	50.0[b]			14.3	7.1	7.1	7.1	7.1			7.1		
DF		63.6				18.2	9.1		9.1				
RW			72.2	5.6						5.6	5.6		11.1
HT	10.0			50.0		10.0		30.0					
BGG	10.0	5.0			45.0		20.0	10.0	5.0			5.0	
SV				30.8	15.4	30.8		15.4				7.7	
VW		6.7			13.3		66.7	13.3					
BTG	14.3			10.7	17.9	7.1	17.9	25.0				7.1	
GTT			10.0		13.3		10.0		40.0	3.3	3.3		20.0
RST	5.0	5.0	40.0		10.0		10.0		10.0	15.0			5.0
VS					5.9						76.5	5.9	11.8
CS	22.2							5.6			22.2	50.0	
BS			5.3						5.3	5.3	5.3		78.9

[a] See Table 2 for symbols of bird species.
[b] Percentage of correctly classified cases for each species lies along the diagonal.

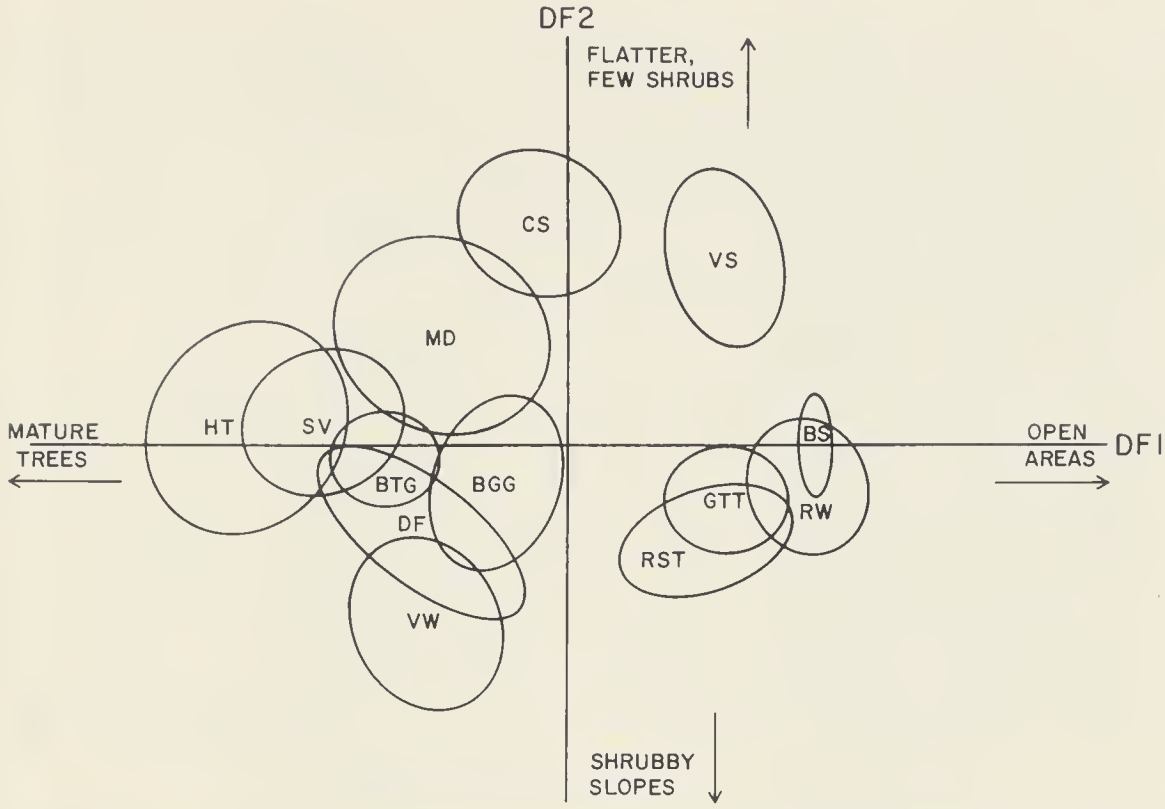

FIG. 2. Ninety-five percent confidence ellipses for the bivariate means of 13 bird species based on discriminant functions 1 and 2. See Table 2 for key to species' symbols.

variables selected by the DDA. Birds of open areas, such as Rufous-sided Towhees, were most frequently misclassified as Rock Wrens; Green-tailed Towhees were most frequently misclassified as Brewer's Sparrows. These species were all close to one another in discriminant 3-space (Fig. 1).

Habitat relationships and habitat-niche breadth.—The habitat-niche (Smith 1977) of each species was compared to that of other species by comparing distances (the Mahalanobis distance) between group centroids in multivariate habitat space. There was a significant difference ($P < 0.05$) in habitat-niche between 74 of the 78 species pairs (Table 5). Large F values correspond to large differences between species in multivariate space and indicate segregation in habitat space. Smaller F values suggest less separation in habitat space. Virginia's Warbler-Dusky Flycatcher ($F = 2.10$) showed less separation, for example, than did Black-throated Gray Warbler-Rock Wren ($F = 10.58$). Species pairs that overlapped considerably (nonsignificant F values) included Solitary Vireo-Hermit Thrush, Green-tailed Towhee-Rufous-sided Towhee, Brewer's Sparrow-Rufous-sided Towhee, and Brewer's Sparrow-Green-tailed Towhee. The sparrow and two towhees were often found in natural openings or chained areas where territories were adjacent or appeared to overlap. Solitary Vireo and Hermit Thrush were frequently found in similar woodland habitats where

TABLE 5

SIGNIFICANCE LEVELS (*F* VALUES) FOR PAIRWISE CONTRASTS BETWEEN 13 SPECIES OF BIRDS BREEDING IN NORTHWESTERN COLORADO

	MD	DF	RW	HT	BGG	SV	VW	BTG	RST	GTT	CS	BS
DF[a]	4.29[b]											
RW	7.41	7.39										
HT	3.06	3.69	10.16									
BGG	2.72	3.21	7.44	5.23								
SV	2.96	3.03	9.54	NS[c]	3.25							
VW	4.42	2.10	7.91	4.66	2.14	3.72						
BTG	2.59	3.44	10.58	3.15	2.16	2.09	2.23					
RST	5.25	4.87	2.21	7.79	3.69	6.85	4.29	6.61				
GTT	5.92	5.29	3.27	9.67	3.67	8.21	5.93	8.93	NS			
CS	2.48	4.74	6.95	5.53	4.38	4.85	6.66	5.00	6.03	6.57		
BS	6.55	7.79	1.87	10.13	6.11	8.91	8.51	10.05	NS	NS	6.47	
VS	5.67	6.44	5.29	10.10	5.31	7.53	8.35	8.53	4.71	3.98	2.90	3.40

[a] See Table 2 for symbols of bird species.
[b] Each *F* has 17 and 204 degrees of freedom and corresponds to a significance test for the Mahalanobis distance between species.
[c] NS = not significant ($P > 0.05$).

the trees were large, percentage canopy cover was high, and some dead trees were present.

Ninety-five percent confidence ellipses graphically illustrate habitat relationships among the 13 species (Fig. 2). Such ellipses are functions of the variance and covariance of discriminant scores for DF1 and DF2 and will contain the true mean for each species in discriminant 2-space 95% of the time. Some species and species-groups were clearly segregated within the forest type. For example, species that occupied open areas were distinct from the woodland species, and Vesper Sparrow habitat space was well-separated from that of all other species. At least some overlap existed for all other species. In open areas, the greatest overlap occurred between the two towhees and between Brewer's Sparrow and Rock Wren. In woodlands, Hermit Thrush and Solitary Vireo overlapped considerably, suggesting selection for similar habitats. Black-throated Gray Warbler and Dusky Flycatcher each overlapped with five other species, reflecting their central positions in woodland habitat space. Chipping Sparrow was well segregated from the other woodland species along DF2, preferring flatter habitats where shrubs were smaller and less diverse.

As the variance of DF1 and DF2 is a component of the confidence ellipses, these may be thought of as measures of variability in resource use, or as measures of habitat-niche breadth (Pianka 1974). The larger the confidence ellipse, the more variable the species is in resource use. Mourning Dove and Hermit Thrush had the largest confidence ellipses, indicating wide latitude in habitat selection regarding the dimensions described by DF1 and DF2. Brewer's Sparrow had the smallest confidence ellipse, suggesting a narrow range of variability along DF1 and DF2. This species had an especially narrow habitat-niche breadth along DF1, reflecting its habit of nesting in large, monotypic stands of sagebrush. Blue-gray Gnatcatcher, reported in other studies as being a habitat generalist (James 1971, Whitmore 1975), had an intermediate habitat-niche breadth in pinyon-juniper.

Two group DDA: habitat associations.—Species breeding in chainings or natural openings within pinyon-juniper woodlands were positively associated with measures of shrubbiness, openness, percentage log cover, small trees, distance from a habitat edge, and slope (Table 6). Coefficients with the largest positive values for Vesper Sparrow were shrub density (SHRBDEN) and openness (BITZERO), whereas the highest negative values were for shrub dominance (SHRBDOM) and distance from an edge (EDGDIST). Vesper Sparrows could be expected to have high positive scores along this discriminant axis since they were found near edges, and in areas of little to moderate slope characterized by dense, small shrubs, and low shrub diversity. These findings agree with those of Best

TABLE 6

SUMMARY OF THE TWO-GROUP DISCRIMINANT ANALYSES

	Standardized discriminant function coefficients[a]												
Variables	MD	DF	RW	HT	BGG	SV	VW	BTG	GTT	RST	VS	CS	BS
CANHT	–	–	–	–	–	0.49	–	–	−0.71	−0.58	–	–	–
GRNDSP	–	–	–	–	–	–	–	–	–	−0.40	–	0.45	–
PGCOVER	–	–	–	–	–	–	–	−0.43	–	–	–	0.44	–
PBARE	–	−0.50	–	–	–	–	–	–	–	–	–	–	–
PLITTER	–	−0.45	–	–	–	–	0.34	–	–	–	–	–	–
PCANOPY	–	–	–	–	–	–	–	1.00	–	–	−0.36	–	–
PLOG	–	–	0.39	–	–	–	–	–	0.40	–	−0.37	–	–
PDEADTR	0.80	–	–	–	–	–	–	–	–	–	–	–	–
BITPL	–	–	–	0.34	–	–	–	–	–	–	–	–	–
BITJL	–	–	−0.55	–	–	–	–	–	–	–	–	–	–
BITOL	–	–	–	–	–	–	0.46	−0.28	–	–	–	–	–
BITPD	–	–	–	0.25	–	–	–	–	–	–	–	–	–
BITJD	−0.50	–	–	–	–	–	–	–	–	–	–	–	–
BITDEAD	–	–	–	–	0.40	–	−0.31	–	–	–	–	–	–
BITPH	0.31	–	–	–	–	–	–	−0.28	–	–	–	–	–
BITHALF	–	–	–	−0.27	–	–	–	–	–	–	–	–	–
BITZERO	–	–	–	–	–	–	–	–	–	–	0.44	–	0.68

TABLE 6
CONTINUED

Variables	Standardized discriminant function coefficients[a]												
	MD	DF	RW	HT	BGG	SV	VW	BTG	GTT	RST	VS	CS	BS
DENSTYA	–	–	0.30	–	–	–	–	−0.31	–	–	–	0.32	–
DENSTYB	–	–	–	–	0.48	–	–	–	–	–	–	–	–
DENSTYC	0.35	–	–	–	–	–	–	–	–	–	–	–	–
DENSTYE	–	0.42	–	0.88	−0.52	0.63	–	−0.61	–	–	–	−0.40	–
DENSTYF	−0.43	–	–	−0.52	–	–	–	–	–	–	–	–	
DENSTYG	0.65	–	–	–	–	–	–	–	–	–	–	–	–
SHRBHT	–	–	–	–	–	–	–	–	–	0.41	–	–	–
SHRBDIM	–	–	–	–	–	–	–	–	–	–	–	−0.30	0.27
SHRUBSP	–	–	–	–	0.81	–	0.36	–	0.72	–	−0.21	−0.46	−0.23
SHRBDEN	–	–	–	–	–	–	–	–	–	–	1.00	–	–
SHRBDOM	–	0.36	–	–	–	–	–	–	–	–	−0.77	–	–
EDGDIST	–	−0.39	–	0.47	–	–	–	–	–	0.40	−0.50	–	0.31
SLOPE	−0.42	0.68	0.40	–	–	–	0.53	0.38	−0.25	–	−0.31	–	−0.46
ALT	–	0.34	−0.92	–	–	–	–	–	–	–	–	–	–
EWDIREC	–	–	–	–	–	–	–	–	–	–	0.39	–	−0.37

[a] Coefficients indicate relative contributions of habitat variables to discriminant functions comparing nonoccupied habitat to habitat occupied by each species.
[b] See Tables 1 and 2 for descriptions of habitat variables and key to bird species' symbols.

(1972) who found Vesper Sparrows in sagebrush-grassland associations; however, in the Sierra Nevada, Verner and Boss (1980) reported Vesper Sparrows being associated with early successional stages lacking shrubs. In Montana, Reed (1986) also found Vesper Sparrows in a shrubless grassland, but as in this study, they were found where the vegetation was short and dense, and they avoided areas where vegetation was tall and patchy.

Rufous-sided Towhees were positively associated with distance from a habitat edge (EDGDIST) and large shrubs (SHRBHT). They were negatively associated with canopy height (CANHT) and ground species richness (GRNDSP). This matches the presence of towhees in shrubby habitats far from edges where average canopy height and the number of ground species was low. In Arkansas, Rufous-sided Towhees were birds of open-country habitats (James 1971), and in Missouri, they were influenced by litter coverage and woody stems <2.5 cm dbh (shrubs and saplings) (Kahl et al. 1985). Other studies also document the dependence of Rufous-sided Towhees on a well-developed shrub understory (Shugart and James 1973, Nolan 1963, Davis and Savidge 1971).

Green-tailed Towhees selected habitats on the basis of shrub species richness (SHRBSP) and percentage log cover (PLOG). They were negatively associated with canopy height (CANHT) and slope (SLOPE). Whereas canopy height was unimportant and shrubs were important to both towhees, Rufous-sided Towhees were influenced by large shrubs and Green-tailed Towhees were influenced by shrub species richness. Green-tailed Towhees were attracted to small patches of dense shrubs in the Sierra Nevada (Verner and Boss 1980); and in Washington and Oregon, Green-tailed Towhees were "low to moderate shrub-form" nesters (Thomas 1979). In this study, they were especially common in sagebrush-dominated openings within pinyon-juniper woodland. Green-tailed Towhees are frequent inhabitants of sagebrush habitats and are considered sagebrush near-obligates (Braun et al. 1976).

Rock Wrens selected areas with high percentage log cover (PLOG), density of small trees (DENSTYA), and slope (SLOPE). They were negatively associated with live junipers (BITJL) and high altitude (ALT). This association matches the Rock Wren's presence in low-altitude chainings where log cover (slash) and small tree density were high. Rock Wrens are characteristic of early successional habitats (Bent 1948, Thomas 1979) and are often associated with rocky outcrops, but may also use slash piles in pinyon-juniper chainings (Sedgwick and Ryder 1986).

Brewer's Sparrows selected open (BITZERO) habitats with large shrubs (SHRBDIM) and were typically found far from edges (EDGEDIST). Their habitats were also characterized by small slopes (SLOPE) and low shrub

species richness (SHRBSP). Brewer's Sparrows occurred in sagebrush-grasslands in Montana (Best 1972) and were characteristic of large sagebrush openings in pinyon-juniper woodland in the Piceance Basin. Wiens and Rotenberry (1981) found Brewer's Sparrows at their highest densities in open, flatland habitats and where shrub diversity was low, as in Colorado. Other habitat associations of Brewer's Sparrows include positive correlations with shrub cover, bare ground, and forb cover, and negative correlations with grass and litter cover and the amount of rockiness (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981).

Woodland species were strongly associated with high canopies, high percentage canopy cover, live and dead pinyons, and high tree densities. Solitary Vireos selected habitats on the basis of canopy height (CANHT) and large tree density (DENSTYE), and they were associated with only the most mature stands of pinyon-juniper. In the Sierra Nevada, Solitary Vireos used shrubby understories and low to intermediate canopy cover (Verner and Boss 1980), and they used intermediate-stage conifer communities in the Blue Mountains of Oregon and Washington (Thomas 1979). This species may be more of a generalist regionwide than indicated by the results of any particular study.

Hermit Thrushes also used mature stands of pinyon-juniper, being favored by large trees (DENSTYE), and by live (BITPL) and dead (BITPD) pinyons. They selected interior woodland habitats and avoided sites near edges (EDGDIST). This species is typically associated with mature, forested habitats and forest interiors (Thomas 1979).

Black-throated Gray Warbler habitat was distinguished from nonhabitat by relatively steeper slopes (SLOPE), and higher canopy cover (PCANOPY). Areas with steep slopes are typically not chained, and these situations were favored by Black-throated Gray Warblers. Conversely, Verner and Boss (1980) report some preference for areas with low percentage canopy coverage, and Thomas (1979) describes Black-throated Gray Warblers as nesters of "0.3 to 1.2 m high shrub-form habitats" within the conifer zone. Apparently, this species is flexible in its choice of canopy and shrub coverage.

Dusky Flycatchers selected habitats on the basis of shrubby slopes (SHRBDOM, SLOPE) where large trees (DENSTYE) were present. They were also influenced by ground cover (PBARE, PLITTER), and preferred edge situations (EDGDIST). Dusky Flycatchers are typically associated with shrubby habitats with scattered trees or occur in open conifer forest (Grinnell et al. 1930, Sumner and Dixon 1953).

Virginia's Warblers showed a strong relationship with steep slopes (SLOPE), litter cover (PLITTER), live Gambel's oak (BITOL), and shrub species richness (SHRBSP). They were negatively associated with dead

trees (BITDEAD). In the Piceance Basin, they were found almost exclusively in Gambel's oak chapparal or in oak-covered draws within pinyon-juniper woodland. Various shrub-form associations are favored by Virginia's Warblers throughout the West, including mountainmahogany, snowberry, willow (*Salix* spp.), sage, and plum (*Prunus*) (Bent 1953).

Chipping Sparrows selected a more open habitat where small trees (DENSTYA), ground species richness (GRNDSP), and ground and green cover (PGCOVER) were above average. They were negatively associated with shrub size (SHRBDIM), large tree density (DENSTYE), and shrub species richness (SHRBSP). Chipping Sparrows were characteristic birds of open country in Arkansas (James 1971) and were associated with small shrub patches in the Sierra Nevada (Verner and Boss 1980).

Mourning Doves were associated with moderate slopes and areas where trees were large (DENSTYG) and dead and dying trees (PDEADTR) were present. In the Sierra Nevada of California, this species preferred stands with low percentage canopy cover (Verner and Boss 1980). Mourning Doves are habitat generalists (Stauffer and Best 1980) occurring in a wide variety of habitat types.

Blue-gray Gnatcatchers were positively associated with 3 habitat variables—shrub species richness (SHRBSP), small trees (DENSTYB), and dead trees (BITDEAD). Both James (1971) and Whitmore (1975) found this species to be a habitat generalist showing wide latitude in habitat use. Similarly, this species was observed in all forest habitats in Missouri, and habitat selection seemed random (Kahl et al. 1985). In this study, their broad latitude in habitat selection is reflected by their central position in woodland habitat space and their association with both shrubby, open chainings (SHRBSP and DENSTYB) and with mature pinyon-juniper (BITDEAD). In Tennessee, Anderson and Shugart (1974) found Blue-gray Gnatcatchers to be associated with understory biomass.

CONCLUSIONS

Two broadly defined groups of birds can be identified in this study: woodland species and open-area species. Hermit Thrushes, Solitary Vireos, and Black-throated Gray Warblers, for example, overlapped extensively in woodland habitat space and were generally dependent on forest overstory, being associated with late-successional stages of the pinyon-juniper type. All would be especially susceptible to chaining. Similarly, Green-tailed Towhees, Rufous-sided Towhees, and Rock Wrens showed extensive overlap and shared habitat associations in open-area habitat space. These species are early successional species and would benefit from chaining.

Species with extreme values along the discriminant axes were also identified; these species were most obviously distinct from all other species

and their habitat preferences were most easily described. Virginia's Warblers, for example, preferred shrubby, oak-covered slopes with high grass, forb, and shrub cover. Chipping Sparrows preferred edge habitats intermediate between woodlands and openings, and Hermit Thrushes were found only in the most mature woodland situations far from habitat edges. Vesper Sparrows favored small shrubs in relatively flat areas. Habitat-niche exclusiveness is reflected in the high rates of correct classification of cases for these species. Other woodland species (Solitary Vireo, Black-throated Gray Warbler) and species of open areas (Green-tailed Towhee, Rufous-sided Towhee) occupied central positions in woodland and open-area habitat space, respectively. Habitat-niches of these species were not well segregated, and their habitat preferences were less unique.

The two-group DDA provided greater resolution and identified habitat relationships more specifically. Associations of species with specific habitat variables suggest varying susceptibilities to habitat change. The association of Hermit Thrushes, for example, with mature woodland and great distance from a habitat edge suggests that they would be especially susceptible to forest fragmentation (cf. Ambuel and Temple 1983). Dusky Flycatchers, on the other hand, were associated with edges and a diverse understory of large shrubs, and would benefit from the creation of small openings in the woodland overstory. Vesper and Brewer's sparrows both were associated with stand openness and would benefit from the creation of relatively large openings in pinyon-juniper woodland. Both the Green-tailed and Rufous-sided towhees were favored by the presence of shrubs, and habitat alterations creating shrublands would benefit these species. Management actions that change the structure or coverage of the vegetation should consider those variables that loaded highly on the discriminant functions and that most strongly influenced habitat selection.

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GROWTH AND DEVELOPMENT OF SORA AND VIRGINIA RAIL CHICKS

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ABSTRACT.—Sora (*Porzana carolina*) and Virginia Rail (*Rallus limicola*) chicks were observed in the wild and in captivity. In both species the chicks are precocial in ground and aquatic locomotion, semiprecocial in feeding themselves, and altricial in feather development, flight, and possibly thermoregulation. Sora chicks had more conspicuous head coloration and begging display than did Virginia Rail chicks, and they were slightly slower in attaining feeding self-sufficiency. *Received 7 Oct. 1986, accepted 23 Jan. 1987.*

The newly hatched young of most Rallidae are covered with black down and are precocial (Ripley 1977). There are, however, considerable morphological differences in the head coloration among species of rails, and even within some subspecies. Boyd and Alley (1948) made the first extensive comparison of the coloring of young rails in their attempt to evaluate the function of bright coloration. Their search was hampered both by lack of species descriptions and by descriptions of chicks of unknown age. The latest coverage by Ripley (1977) still lacks descriptions of many species of rail chicks and their degree of parental dependence. Until more species are described, the function and adaptive value of these differences remain unknown.

Here, I describe the morphological and behavioral development of the chicks of the Sora (*Porzana carolina*) and the Virginia Rail (*Rallus limicola limicola*) of known age.

METHODS

Newly hatched Sora and Virginia Rail chicks were observed in the field and in captivity in Iowa and Minnesota during the 1963–1969 nesting seasons (Kaufmann 1977, 1983). Causal observations of newly hatched young were made during the inspection of 21 Sora nests and 14 Virginia Rail nests in the field. More intensive observations were made from blinds near one Sora and 4 Virginia Rail nests in the field. Four broods of Soras (17 chicks total) and one brood of 2 Virginia Rail chicks that were raised by their parents in a large flight pen with marsh conditions were also observed. Three Sora and one Virginia Rail pipped eggs were taken, and the chicks were raised by hand in 1966, and 2 Sora chicks were taken from nests and raised by hand in 1969. Chicks were kept in a box along with a saucer of water and a light bulb, and were hand-fed every 2 h from 04:00 until midnight for about one week after hatching at which time they began feeding for themselves.

I mixed 2 hard boiled egg yolks, 1 can of horsemeat dog food, 1 can of nearly all vegetable dog food, and several vitamin drops for rail food. Two Sora and a Virginia Rail chick were

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weighed, and the lengths of their right tarsometatarsi were measured every several days for 5 weeks.

RESULTS

Physical Development

Body growth.—The young of both species gained weight rapidly during their first 5 weeks (Fig. 1A). Their metatarsi and toes grew rapidly and reached adult size by the 3rd week (Fig. 1B). Tarsal lengths (mm) of autumn juvenile and adult Soras were $\bar{x} = 3.13$ (range = 2.65–3.54, N = 58) and of Virginia Rails were $\bar{x} = 3.42$ (range = 3.14–3.60, N = 34).

Eye pigmentation.—The iris of both species is black at hatching and changes to a dark olive during the 3rd week. By the 4th week, it is olive brown, and it is brown by the 8th week. The iris of the adults of both species is reddish brown, but those of Soras change to black during the breeding season (Kaufmann 1983).

Bill color.—The bill of the newly hatched Sora chick is dirty white, with a pure white egg tooth at the tip of the upper mandible and a large blood red cere. The cere, which is soft, is filled with blood, and its color fades within a few minutes of a chick's death. By 2 weeks, the distal half of the bill darkens, the cere becomes dull and deflated, and the base of the lower mandible becomes a pale orange-yellow, while the base of the upper mandible remains a dirty white. The egg tooth is gradually incorporated into the tip of the upper mandible during the 2nd week. At 3 weeks, the cere is nearly gone, and the base of the upper mandible is a soft rose. At 5 weeks, the entire bill is dull greenish-black, with a ring of soft rose at the base. During the 2nd month the bill becomes green and then increasingly yellow; at 3 months, the bill is yellow with a wash of green. During the breeding season, the bill is spectrum yellow, frequently with a patch of rose or orange near the nares. During the nonbreeding seasons, the bill decreases slightly in size and reverts to yellow with a wash of green.

The bill of the newly hatched Virginia Rail is pale pink, with a narrow band of black just distal to the nares. The white egg tooth at the tip of the upper mandible is less conspicuous than is that of the Sora. The bill color remains constant, but the pigment of the center black band expands, so that by the 2nd week the central third of both mandibles is black. In addition, black pigment expands from the base of the lower mandible, and the egg tooth is nearly absorbed into the tip of the upper mandible. At 3 weeks, the lower mandible is black except for the tip. At 1 month, the entire bill is black; at 3 months, the center of the lower mandible is brownish red. In the adult, the lower mandible is nearly all brownish red, as is the lower portion of the upper mandible.

Legs.—The tarsometatarsi and toes of the Sora are a light pink during

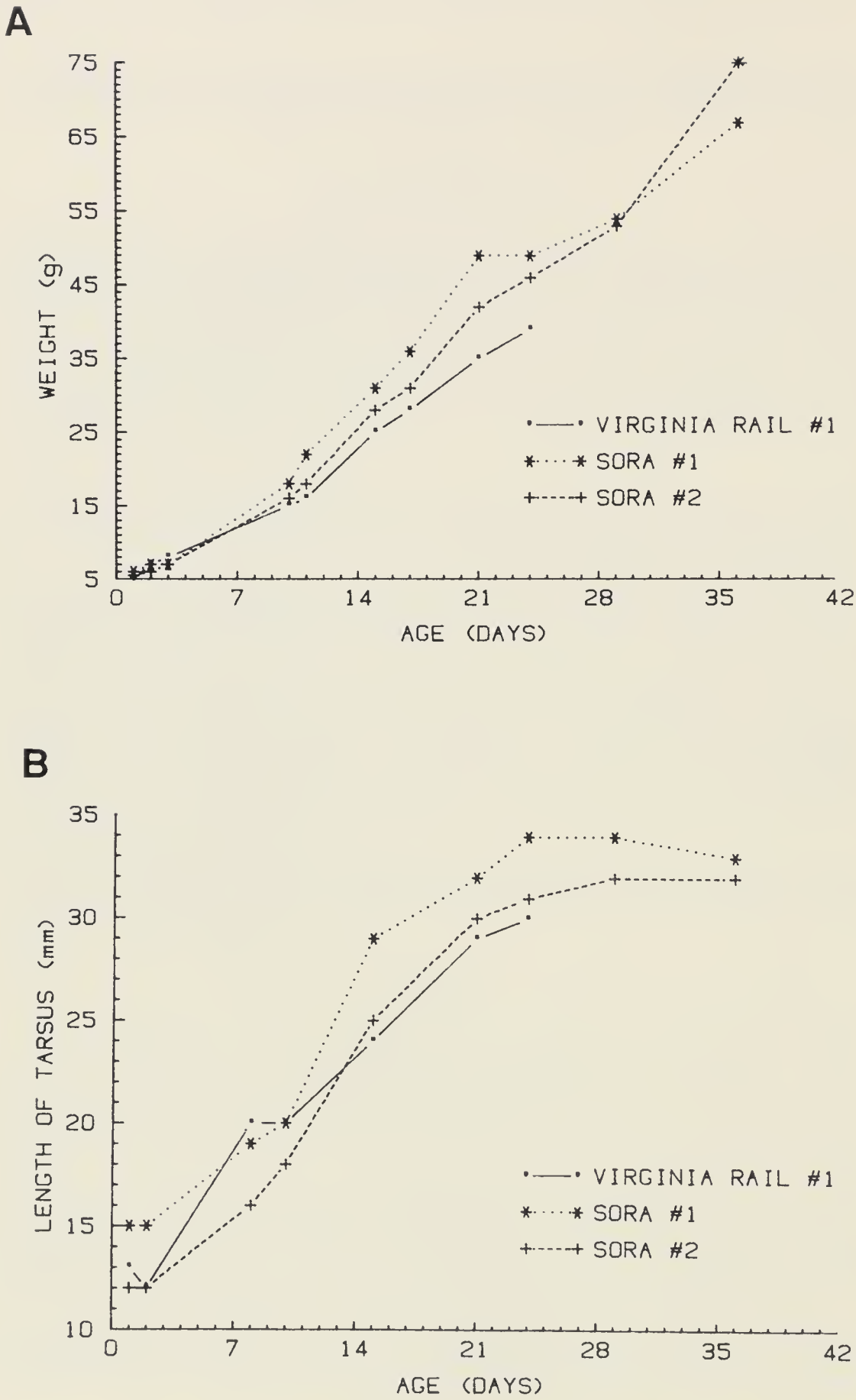

FIG. 1. A. Weight gain of 2 hand-raised Sora chicks and 1 Virginia Rail chick. B. Growth of tarsometatarsi of 2 hand-raised Sora chicks and 1 Virginia Rail chick.

the 1st week, changing to a dull gray at 2 weeks, to gray-green at 3 weeks, to dark yellowish-green at 3½ weeks, and to yellow-green at 4 weeks. The tarsi and toes of the Virginia Rail change color more gradually. Initially they are dark brownish black and remain so far a month; they become dusky-brown during the 2nd to 3rd month.

Plumage and skin.—The chicks of both species are almost entirely covered with black down that has a greenish gloss in sunlight. The Sora chick has a long tuft of chrome orange down at the base of its lower mandible, which is conspicuous during its first week but disappears almost entirely by the 2nd week. Both species have bare areas on the crown of their heads and around their eyes, but these areas are more conspicuous in the Sora. The entire crown of the Sora chick is nearly devoid of down, and it remains bare until the 3rd week. The down on the posterior of the crown of Virginia Rail chicks is less dense than elsewhere, and appears most bald during the 2nd and 3rd weeks. Both species have dark bluish-black pigmented skin around their eyes, covering nearly the entire side of their heads. This is more conspicuous in Sora chicks because there is more bare area around the eyes.

Juvenal plumage begins to emerge at 2½ weeks on the breast area of the ventral tract of both species, expanding anteriorly and posteriorly, until the ventral tract is fully emerged by 3½ weeks. Ventral feather tracts are tan in the Sora and sooty black in the Virginia Rail, grading to a cream in the center of the breast in the Sora and to a dirty white in the Virginia Rail. The crural tract emerges several days after the ventral tract; then the femoral, spinal, and capital tracts emerge during the 3rd week. The alar and caudal tracts are the last to develop, emerging during the 3rd to 4th weeks. The 1st winter plumage emerges during the 3rd and 4th months.

Behavioral Development

Hatching, locomotion, and maintenance behavior were similar for Sora and Virginia Rail chicks, and the following descriptions apply to both species. I will point out the differences between the species in begging, feeding, and social behavior. All descriptions apply to observations of both wild and captive chicks unless specifically mentioned.

Hatching.—The first signs of hatching were the appearance of a small area where the eggshells were broken outward, forming a projection on the surface, and the soft, peeping cries of the chicks inside. After 36–48 h chicks broke entirely through the eggshells, and they emerged within 1–1½ h.

Locomotion.—The newly emerged chicks were weak, and could hold their heads up for only a few seconds. After about 6 h, they could remain upright by sitting on their metatarsi and feet, while propping themselves

up with their wings. They moved on both the feet and metatarsi while balancing and pulling with outstretched wings. The claw on the first digit of each wing was used in grasping vegetation to pull themselves forward. By the end of the 1st day, they could scamper down the nest ramp to drink and defecate, and could swim. When I disturbed the nest, the chicks ran off and swam in all directions, and sometimes dived. Chicks over 3 days of age would swim over 5 m, but 1-day-old chicks usually swam for 30–60 cm. Newly hatched chicks, still wet and less than 2-h-old, occasionally swam when I visited a nest. Chicks would swim into the base of a clump of marsh vegetation with their head in the clump and their body floating outside. Wet chicks had difficulty floating. Unless disturbed, the chicks never left the nest the first 3 or 4 days.

At 3 weeks of age chicks were able to jump 30–40 cm high. Chicks were able to fly at 4 weeks, when their flight feathers were nearly developed.

Maintenance behavior.—For about the 1st week, chicks drank by dipping the bill in water, then pointing the bill up. Older chicks and adult rails did not tip the bill up during drinking. Defecation usually followed drinking. Chicks touched their cloacas to the water for several seconds, defecating while performing a two-wing stretch. For the 1st week, hand-reared chicks continued to defecate in the water. During the 2nd week, defecation in the water gradually diminished. I believe my first attempts to raise rail chicks failed because I did not provide them with water pans sufficiently shallow for them to enter for such defecation.

When they were 1-day-old, chicks performed several comfort movements including yawning, wing-and-leg stretch, body shake, bill scratching, bill shake, and preening of the belly. Bill scratching was unsuccessful until the end of the 1st week when the chicks could balance on one leg.

Although they preened themselves on the 1st day, chicks were preened much more by the adults at this time. Siblings frequently preened each other in the nest. Oiling was not observed until day 18. Bathing by alternately dipping the head and tail up and down into the water occurred at the end of the 1st week. Three or 4 days later bathing was performed more vigorously, with the addition of pronounced flicking up and down of the tail. Several chicks did not bob their heads or thrash their wings until 3–4 days later. At 8 days the two-wing stretch was performed without defecation.

Feeding and begging behavior.—One-day-old Sora chicks begged with loud, plaintive peeping calls and gaping. Gaping first consisted of raising the head and neck upward with the mouth open. By day 2, the chicks pecked at the tip of the parent's bill. The frequency of pecking appeared to increase as the time increased since the young were last fed. Pecking

appeared to stimulate the brooding parent to call "Tug," which probably enticed the other parent to bring food to the nest.

Hand-raised Soras plaintively peeped when they had not been fed for more than an hour. When I approached, they begged to me. Begging consisted of crouching down on the metatarsi, waving the wings vertically, and alternately gaping toward my hand and bowing the head so that the bald forehead faced my hand. The down on the head was depressed, but there were no striking color changes of the bare skin of the head. Soras continued to crouch on their metatarsi while begging long after they were able to stand on their toes. When begging, Sora chicks drew attention to the facial coloration of red cere, ivory bill, orange down beneath the bill, and bald head against the glossy black down by waving their wings.

In the wild, I could not see whether young Soras begged while being fed during the first two days, as their bodies were beneath the parent. I did, however, see begging at age 3 days, as soon as the young were able to run to the parent, which was bringing food to the nest. Adults continued to feed their young for 3 weeks.

Young Virginia Rails did not show elaborate begging behavior. After a period of not being fed, they peeped loudly and pecked at the parent's bill. The brownish red coloration of the lower mandible of the adult's bill appeared to aid in the orientation of this pecking response. Occasionally, the young Virginia Rails waved both wings while begging or being fed, but this was not nearly so marked as in the Sora.

Chicks of the Water Rail (*R. aquaticus*) have a special display, which apparently has an appeasement function (Lorenz 1952). The chick bows its head, flattens the down on the top of its head, and reddens the exposed skin on the head. I never saw the chicks of the Virginia Rail bowing their heads to adults. Although they may have flattened the down feathers of the head and flushed the exposed skin, this was never as conspicuous as that described for the Water Rail, nor did it occur very frequently. Occasionally, captive chicks sleeked their down, and then the skin appeared to be more pinkish than usual. The only time I observed definite sleeking and possible flushing was when a wild female picked up its youngest chick by the head and carried it back to the nest in her bill.

Hand-raised Soras began to feed themselves at the same time as did the Virginia Rails, but they appeared to be slower in obtaining full self-sufficiency. Chicks of both species pecked at the food on day 2, but were unable to pick up food until day 3. Between days 4 and 7, chicks became adept at feeding, and by day 7 they could feed themselves. Virginia Rail chicks ate a larger portion of food by themselves than did the Sora chicks during days 4 to 7.

Although the Virginia Rail chicks appeared to be able to pick up food

within a week, adults continued to feed them for some time. Free ranging juveniles over a week old were seen being fed by adults, and captive juveniles in the flight pen were fed by their parents for over a month after hatching.

Probing for food and washing food by Virginia Rail chicks began later than did self feeding. When Nice (1962) first provided mud to her 22-day-old juvenile rails, they probed immediately. The juveniles in the breeding pen were not observed probing until they were older than this. The hand-reared chick first washed its food at the age of 16 days.

The food items brought by the adults are presumably important in influencing the juvenile's ability to recognize food. The hand-reared rails of both species readily ate canned dog food from hatching. Wild juveniles over one month old I caught would not eat dog food unless I continued to mix in live invertebrates (crayfish and dragonfly nymphs) for over a week.

Social behavior.—The following response of rail chicks was unlike the classical response of young Anatidae. Chicks of both species usually left the nest by following a parent, but frequently lagged behind. As each parent approached and then left the nest, it was followed by some of the chicks. Typically, one to 4 chicks continued to follow within a meter of each adult. Other chicks stopped to preen, feed, or rest and were soon left alone or in small groups. Chicks without an adult appeared to be contented and frequently returned to the nest before a parent did. Hand-raised rails ran toward me for feeding and, when I released them outside, they remained within a meter of me. At 3 weeks they began to withdraw at my approach. At 25 days they crouched at my approach, and defecated when I picked them up. At 30 days, they flicked their tails at the sight of me, and at 37 days the Soras pecked me when I handled them.

The appearance of aggressive behavior varied greatly in the captive birds. One hand-reared Sora, 12 h older, vigorously pulled the downy chrome orange beard of its sibling on the 1st day. Sora chicks in the flight pen actively chased the much larger juvenile Virginia Rails at 18 days. Nice (1962) observed her hand-reared Soras pecking strange chicks at the age of 14 days, allopreening at 17 days, and play-fighting at 18 days.

Overt aggression was not observed among juvenile Virginia Rails. At 3 days of age, however, hand-reared Virginia Rails pecked the beards of the 3-day-old Soras when the Virginia Rail was hungry and appeared to dominate them. Nice (1962) noticed that her Virginia Rails pecked strange birds introduced to the group at 16 days. Nice also observed allopreening at the age of 15 days in her Virginia Rails and "play-fighting" at the age of 31 days.

Rail chicks appear to depend upon their parents for warmth and dryness

for an extended period of time. Young chicks quickly became waterlogged when they swam from the nest, presumably because they had not received oiling from their parents. Older chicks were brooded by their parents for about a month. The hand-raised Virginia Rail died at 25 days when I placed it outside overnight. The night was cool (for an Iowa July) and a rain shower fell.

DISCUSSION

The morphological and behavioral development of Sora and Virginia Rail chicks closely parallel each other. Nice (1962) classified the maturity at hatching in rails as the fourth category of precocial, i.e., birds which follow their parents and are fed by them. I would describe rail chicks as precocial in that they are down covered and capable of running and swimming the 1st day; semi-precocial in that they begin feeding themselves by the 3rd day and reach self-sufficiency in picking up food by the 7th day; and altricial in their development of wing limbs, flight feathers, and in achieving thermoregulation.

The head coloration of young Soras is strikingly more conspicuous than that of Virginia Rail chicks. Boyd and Alley (1948) remark that bright head coloration is more common in *Fulica, Porphyrio,* and *Gallinula* and that it is rare in *Rallus* and *Porzana.* They suggest that the function of such coloration is to stimulate the adults to feed the young. The presence or absence of such coloration in the various species of rails, however, should be viewed as being but one aspect of the entire repertoire of ecological adaptations of the species. The function of head coloration in rails remains unknown, and further comparative work on food habits, clutch size, and asynchrony of hatching is needed. A comparison of *R. l. limicola* with *R. l. aequatorialis* might prove useful, as the young of the latter subspecies have orange and scarlet bill markings, which are absent in the former.

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HABITAT AND MOVEMENTS OF BREEDING YELLOW RAILS

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ABSTRACT.—Four pairs of Yellow Rails (*Coturnicops noveboracensis*) were radiotracked (1039 locations) in May–August 1980 at Seney National Wildlife Refuge, Michigan, to identify characteristics of breeding habitat and its use by Yellow Rails. Vegetation at nesting sites was dominated by *Carex lasiocarpa* (>90% of basal stems) in wet sedge meadows, which comprised nearly 90% of the 30-ha study area. Water depth in the meadows was 20–30 cm in spring, but standing water was absent by mid-July. Male activity areas overlapped and averaged 7.8 ha (range = 5.8–10.5) during preincubation and incubation; areas used by females averaged 1.2 ha (range = 1.0–1.7) during preincubation but declined to 0.3 ha during incubation. *Received 21 Oct. 1986, accepted 9 Feb. 1987.*

The Yellow Rail (*Coturnicops noveboracensis*) is difficult to observe because of its secretive habits, reluctance to fly, and preference for remote areas. This rail is widely distributed in northern North America and is highly sought after by bird watchers, but little is known about its habitat, nesting requirements, breeding population densities, or behavior on the breeding grounds (Anderson 1977). Objectives of our study were to ascertain characteristics of breeding habitat and its use by Yellow Rails.

STUDY AREA

The study was done in May–August 1980 at the Seney National Wildlife Refuge (NWR), Schoolcraft County, in the Upper Peninsula of Michigan (46°15′N, 86°00′W). The principal study site was 0.4 km from the west end of Marsh Creek Pool. The Marsh Creek Pool Study Area (MCPSA) was chosen because in earlier surveys it had the highest concentration of calling Yellow Rails on the NWR. MCPSA was a seasonally flooded wet sedge meadow marsh, with water depths of 30 cm or more in the spring that became moist soil by midsummer.

The physiography of the MCPSA was similar to that of the surrounding area. Sand knolls, apparently extinct dunes (Heinselman 1965), were interspersed within the sedge marsh. The vegetation on the knolls was dominated by red pine (*Pinus resinosa*) and white pine (*P. strobus*). Swamp birch (*Betula pumila*), speckled alder (*Alnus rugosa*), and quaking aspen (*Populus tremuloides*) ringed the edges. Bracken fern (*Pteridium aquilinum*) and blueberries (*Vaccinium* spp.) were the principal ground cover, especially in areas burned in 1976.

The principal marsh plant was a tall, mat-forming sedge (*Carex lasiocarpa*) that dominated the extensive wet sedge meadows throughout the refuge. Small colonies (<0.5 ha) of bluejoint grass (*Calamagrostis canadensis*) and rushes (*Juncus* spp.) were in slightly elevated or depressed areas, respectively. Willows (*Salix* spp.), about 1 m in height, dotted the marsh portion of the entire study area, and higher densities occurred on the drier sites.

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METHODS

The 30.25-ha MCPSA was gridded into 121 50 × 50-m sections. Stem density was determined by randomly locating 100 0.05-m^2 plots, each 10 × 50 cm. Height of vegetation and of the senescent sedge layer (from previous growing seasons) from the substrate was measured to the nearest centimeter. Stems were counted and classified as *C. lasiocarpa*, *Carex* spp. (other than *lasiocarpa*), *Juncus* spp., *Calamagrostis canadensis*, Gramineae (other than *C. canadensis*), herbaceous species, *Salix* spp., and other woody species. Four 50 × 50-m stem-density sample plots were centered around locations of calling males south of the MCPSA. Within each plot 10 random locations were chosen, and at each location all stems within 0.5-m^2 (2 plots) or 0.25-m^2 (2 plots) plots were counted and assigned to the same classes as described above.

Male Yellow Rails were attracted at night (22:00–04:00 h) by striking two small stones together to imitate the territorial call of the male. This caused males to approach an area illuminated by flashlights closely enough to be captured with a hand net. A pointing dog was used to locate all female rails and males that did not respond to the imitation call; these birds were captured with hand nets.

Radiotransmitters with doubler or tripler circuits (Model MP1145LD, Wildlife Materials, Inc., Carbondale, IL) were attached to the birds with sutures, harness, or cyanoacrylate adhesive (Stenzel 1982:14–16) to monitor movements. Permanent locations for obtaining bearings on transmitter signals were established in the MCPSA to facilitate plotting of locations and to minimize disturbance to birds and habitat. A plotted location was derived from 2 to 4 bearings taken ≤20 minutes apart; details for determining the location point were given by Stenzel (1982:16–18). The area of activity was derived by connecting the outermost points to construct a minimum-area polygon (Mohr 1947).

RESULTS AND DISCUSSION

Habitat characteristics.—The MCPSA was dominated by a sedge, *C. lasiocarpa*. Sand knolls and slightly elevated areas dominated by bluejoint grass represented less than 12% of the study area. Small stands of cattail (*Typha angustifolia*) (total area <350 m^2, N = 2), *Juncus* spp. (total area <270 m^2, N = 2), and swamp birch (total area <700 m^2, N = 3) comprised less than 1% of the area. Standing water and soil moisture generally declined with distance from Marsh Creek Pool, but isolated wetter areas containing concentrations of *C. lasiocarpa* occurred north and northwest of sand knolls, which served as natural impoundments to the southeasterly flow of water (Bart et al. 1984).

Stem density of plants in the sample plots was higher at the MCPSA than at other sites examined (Table 1). All sites sampled were comprised of >90% *C. lasiocarpa*. This sedge occurs widely throughout Michigan and is characterized by its well developed rhizome system that forms extensive mats under black spruce (*Picea mariana*), tamarack (*Larix laricina*), and northern white cedar (*Thuja occidentalis*) (Voss 1972).

Water depths on the MCPSA in April–May 1980 varied from 20 to 30 cm and diminished to 5–8 cm by mid-June; by early July standing water was not present, but the soil remained saturated throughout the field

TABLE 1
STEM DENSITIES IN BREEDING YELLOW RAIL HABITAT, MARSH CREEK POOL STUDY AREA, SENEY NWR, MICHIGAN, 1979–80

Sample site	Plot size (m^2)	N	Vegetation	Stems/plot ± SE	Calculated stems/m^2
Marsh Creek Pool study area	0.05	100	*C. lasiocarpa*	63.2 ± 2.7	1265
			Juncus, Carex, and Gramineae spp.	4.5 ± 0.8	90
			Forbs and woody spp.	2.2 ± 0.4	43
			All vegetation	70.0 ± 2.4	1398
Calling male sites 1, 2	0.50	20	*C. lasiocarpa*	368.9 ± 24.6	738
			Other	33.8 ± 1.6	67
			All vegetation		805
Calling male sites 4, 5	0.25	20	*C. lasiocarpa*	160.4 ± 13.2	641
			Other	7.6 ± 3.1	30
			All vegetation		672
Both male sites			All vegetation		739

season. In 1979 snowfall was deep and late in melting, resulting in high spring water levels. Standing water was present throughout the 1979 season in all areas where Yellow Rails were found and averaged 6.5 ± 2.8 cm [SD] (N = 40, 10 samples in each of 4 plots) between 1 and 15 August on the sample plots examined south of Marsh Creek Pool. The greatest water depth we recorded at a Yellow Rail calling site was 46 cm on 4 June 1979, which was higher than the 37-cm spring marsh depth recorded by Stahlheim (1974). Water depths recorded at Yellow Rail nest sites have varied from 5 to 10 cm (Elliot and Morrison 1979, Peabody 1922) to 2 to 4 cm at Seney NWR in 1979 (2 nests) to moist soil (Devitt 1939, Walkinshaw 1939, Terrill 1943, MCPSA in 1980 [5 nests]).

The senescent vegetation formed a permanent canopy that averaged 16 cm above the substrate at the MCPSA. A canopy layer of procumbent *C. lasiocarpa* was present at the seven Yellow Rail nesting sites that we found.

Rail movements.—Ten rails (4 breeding pairs, 1 breeding male, 1 juvenile) were monitored during the 1980 season. We recorded 345 locations for the males, 649 for the females, and 178 for the juvenile. Here we discuss the movements of the 4 mated pairs.

Within one week of their arrival at Seney NWR in 1980 (first male heard calling on 6 May), males established activity areas that did not vary

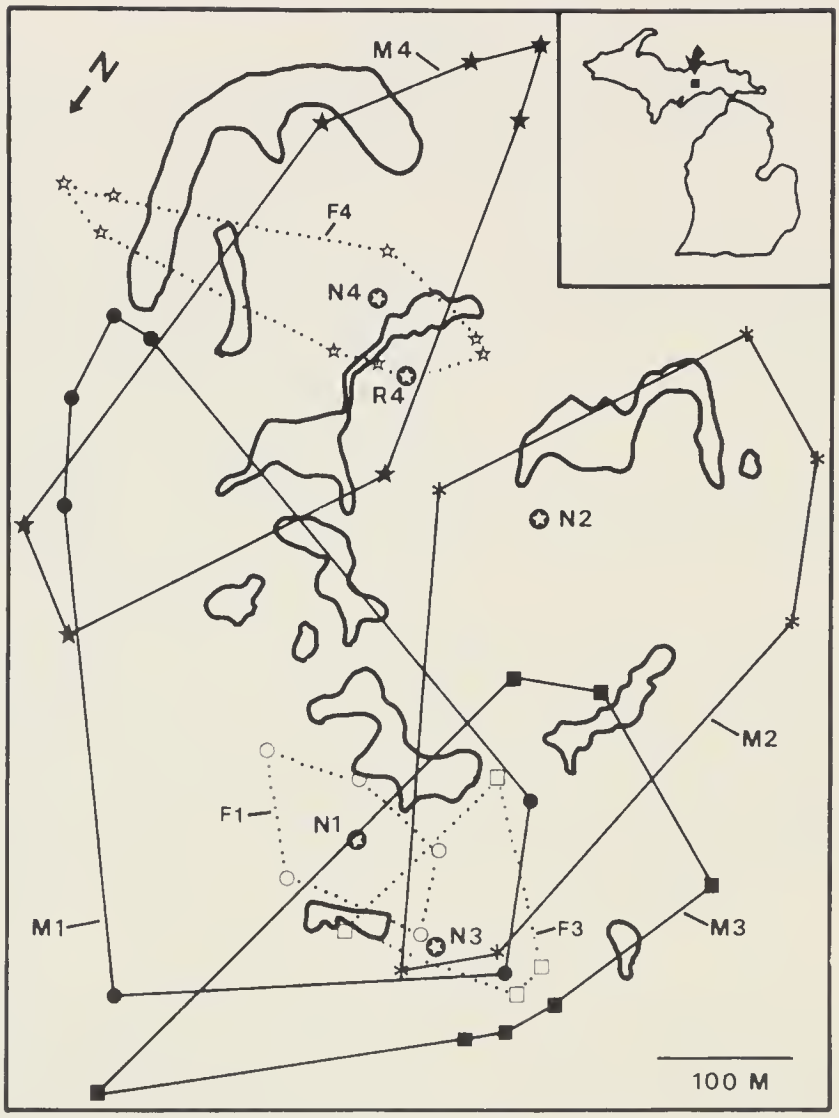

FIG. 1. Movement areas of breeding Yellow Rails during preincubation (males and females) and incubation (males), Seney NWR, Michigan, May–August 1980. Solid symbols connected by lines are male areas; open symbols connected by dotted lines are female areas; symbols of mated pairs are identical. N = nest, R = renest. Irregular areas are sand knolls.

relative to each other for the duration of the breeding season (Fig. 1). Data for male movements during preincubation were combined with those during incubation because Stahlheim (1974) found that calling and patrolling behavior observed during preincubation continued through the incubation period.

Activity areas of mated males averaged 7.8 ha (5.8–10.5), but the distribution of plotted locations within activity areas indicated that the area of frequent use was smaller (Stenzel 1982:44–47). Boundaries of activity areas overlapped, consistent with the suggestion of Bart et al. (1984) that nesting Yellow Rails are slightly gregarious. The pattern of plotted locations of calling males showed the birds were sedentary at night and

TABLE 2
AREA OF MOVEMENT OF FEMALE YELLOW RAILS BEFORE AND DURING INCUBATION, SENEY NWR, MICHIGAN, MAY–JULY 1980

	Preincubation			Incubation		
Female	Date	Area (ha)	No. locations	Date	Area (ha)	No. locations
1	29 May–10 June	1.1	34	11 June–23 June	0.5	145
2				17 June–20 June	0.1	89
3	25 June–29 June	1.0	13	30 June–10 July	0.3	65
4	12 June–5 July	1.7	55	6 July–24 July	0.2	90

mobile during the day. For example, between 06:12 and 20:48 h on 30 May, prior to initiation of incubation, male 1 was near the nest in early evening and early morning, but in the intervening time the total linear distance he moved between plotted points was 983 m, and his greatest straight-line distance from the nest was 375 m. Observations of his calling location on several nights indicated he was near the nest.

The behavior of females during the preincubation period was not readily determined because capturing them at that time was difficult. Females 1, 3, and 4 were captured during egg laying on 28 May, 25 June, and 11 June, respectively (female 2 was captured on 17 June, after she had begun incubating). Female 4 ceased incubation but renested successfully, and her movement patterns were not inconsistent with those of the other two females. During preincubation females were more closely associated with the nest site than were males. Females 1 and 3 stayed within the activity areas of their mates, but female 4 did not (Fig. 1). The average size of the area used by females prior to the onset of incubation was 1.2 ha (Table 2).

Once incubation began, females were closely associated with the nest and incubated through the night. The average detectable distances females 4, 1, and 3 moved from the nest were 21.5, 27.6, and 35.6 m, respectively (SD = 22.6, range = 68.2). Females used an average of 0.3 ha during incubation (Table 2).

Only male 4 retained his transmitter after the eggs hatched, and his movements were more centralized than before hatching. He was in the same location as female 4 (5 plotted locations/bird) on 1 August (16:22 h) to 2 August (19:15 h), a period of more than 23 h. During that time young were heard peeping in the same location; thus male, female, and young were together (we also monitored male 2 at or near the nest of female 2 during hatching and an unmarked male associated with a brood

TABLE 3

MOVEMENTS OF FEMALE YELLOW RAILS DURING POSTHATCH, <8 DAYS (181 H) AFTER LAST YOUNG HATCHED, SENEY NWR, MICHIGAN, 1980

Female	Date and time	No. of plotted locations	Mean distance (m) ± SE from active nest	Area used (ha)
2	20 Jun (13:30 h)–23 Jun (14:54 h)	21	23.6 ± 2.9	0.2
4	24 Jul (13:41 h)–1 Aug (06:17 h)	33	29.7 ± 2.3	0.2

on 27 June [Stenzel 1982:83–85]). Stahlheim (1974) found no association of male and female after incubation began. Males ceased calling on 15 August, and at about that time the bills of males began to darken, suggesting they no longer were in breeding condition (Stahlheim 1974). The area of movement of male 4 after calling ceased was 1.9 ha (45 plotted locations), compared to 6.8 ha he used while males were still calling after eggs hatched (92 locations), suggesting a general decline of encounters with neighboring males as the breeding season waned.

Females 2 and 4 were monitored during hatching of the eggs. Less than 15 h after the last egg hatched, the female led the brood from the nest but remained near the nest for the next few days (Table 3). Female 2 lost her transmitter after 23 June; the only female with young to retain her transmitter more than 5 days after hatch was female 4. During August she moved at intervals of about 1 week between two areas (ca 1.0 and 1.7 ha) separated by a sand knoll in the western portion of her use area (Fig. 1).

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ACTIVITIES OF POSTBREEDING LESSER SCAUP IN SOUTHWESTERN MANITOBA

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ABSTRACT.—Activities of postbreeding Lesser Scaup (*Aythya affinis*) were studied in the prairie-pothole region of southwestern Manitoba. Observations were divided among four time periods: (1) preflightless, (2) flightless, (3) postflightless, and (4) migratory. The only difference in activities between males and females occurred in the preflightless period: males spent more time in comfort activities and swimming and less time feeding than did females ($P < 0.05$). Time spent feeding was low during and after wing molt, and it increased markedly during fall migration. Scaup were most alert before molt and during fall migration. Time allocated to comfort activities was highest during the preflightless and flightless periods, and it declined through the postflightless and migratory periods, closely following molt intensity. Time budgets of postbreeding scaup were similar to those of postbreeding Redheads (*Aythya americana*), except for the greater time spent alert by scaup. Comparisons of other time-budget studies of Lesser Scaup in the same study area indicate that preflightless females in this study spent twice as much time feeding as did females with broods and that time devoted to feeding increased later in the preflightless period. *Received 9 July 1986, accepted 24 Jan. 1987.*

Lesser Scaup (*Aythya affinis*) are among the most abundant breeding diving ducks in the prairie-pothole region. Scaup also are present on these wetlands during spring, molt, and fall migrations, and during the late-summer molt. Previous studies have described the activities of scaup during the prebreeding (Siegfried 1974) and breeding periods (Afton 1983) in this region, but nothing is known of activities after the breeding period.

Most studies of postbreeding ducks have been conducted on areas where large flocks, comprised largely of males, congregate to molt (Bellrose 1976, Young 1977, Peterson 1980, Bailey 1982). Few studies have investigated the activities and ecology of postbreeding birds near the breeding areas or in smaller postbreeding flocks. Information about postbreeding females is particularly lacking. Unlike male ducks, females do not occur in large concentrations during the molt. Information on flightless birds is sparse because of their secretive behavior and the use of secluded habitats while flightless.

I report here on the time budget of postbreeding Lesser Scaup in southwestern Manitoba. Activities were monitored during (1) staging before molt or molt migration, (2) molt and the associated flightless period, and (3) fall migration.

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STUDY AREA AND METHODS

The study was conducted in the prairie-pothole region near Erickson, Manitoba, 240 km WNW of Winnipeg (Austin 1983). Wetlands consisted of shallow ephemeral ponds, seasonal or semipermanent ponds, and permanent lakes (0.5–60.0 ha). Most wetlands were bordered by sedges (*Carex* spp.) and native grasses. Shrubs and aspen (*Populus tremuloides*) were common around larger ponds and lakes. The climate, geology, hydrology, and land use of this region have been described elsewhere (Ehrlich et al. 1956, Johnson et al. 1970, Sunde and Barcia 1975).

The numbers and activities of Lesser Scaup were monitored by weekly censuses on 28 ponds in the study area from mid-May through October 1982 (Austin 1983); these censuses provided an index of the numbers of scaup present in the area. Further observations of birds were conducted on other ponds in the area. The presence of 20 previously marked individuals (Afton 1984) and 8 scaup marked early in this study facilitated the identification of postbreeding events and movements.

Observations were divided into four time periods, based primarily on the observed molt stage of the birds in the flock: (1) Preflightless period, when birds had completed or terminated breeding efforts but had not yet lost flight feathers; (2) Flightless period, when birds had soft growing primaries; (3) Postflightless period, when birds had new flight feathers, and were capable of flight, but were not yet part of migratory flocks; and (4) Migratory period, when birds were in staging flocks or were migrating through the area. Preflightless females were distinguished from incubating or brooding females by behavior (e.g., inactivity for long periods, associations with other female Lesser Scaup). All preflightless observations were conducted on birds in July that were in groups of 2 or more scaup. Flightless birds were obvious by the lack of primary feathers (i.e., observed during wing-flaps or by the different contours of the wing when folded on the body). Observations of birds in time-budgeted flocks and collections from these flocks (Austin 1983) indicated that birds were at all stages of flightlessness, and that these flocks may have included a few late preflightless or early preflightless birds. Observations of postflightless birds occurred before numbers of scaup in the area increased during fall migration.

Fledged juvenile scaup, identifiable with a spotting scope by their dark brown eyes (Trauger 1974), remained separate from adult scaup during the flightless and postflightless stages and were not included in scans. In the migratory stage, juveniles intermixed with adults and were occasionally included in the scans as females because of similarity in plumage. Most adult female scaup, however, could be distinguished from juveniles by their darker plumage and brighter eye color.

Groups of 2 or more Lesser Scaup were monitored from a car or blind for a minimum of 0.5 h and for as long as 4.0 h using binoculars or a spotting scope. Activities were classified as: alert, feed, swim, fly, rest, and comfort movements (Johnsgard 1965). Feeding included dive and dive-pause, dabble, food-handling, and drink. A bird was considered loafing rather than pausing between dives if it did not dive within 15 sec of observation. Comfort activities included preening, bathing, wing flap, wing or leg stretch, shake, or scratch (McKinney 1965). Small sample sizes precluded examination of data among different periods within the day.

I scanned flocks (Altmann 1974) every 3–5 min, and the sex and activity of each bird were recorded on cassette tape. Each individual was observed just long enough to determine the sex and immediate activity (Altmann 1974). The number of males and females underwater (diving) during each scan was determined from the known number of each sex present in the flock. The percentage of time spent in each activity for each sex was calculated for each observation session.

Activity data were transformed for analysis using the arcsine square-root function (Sned-

ecor and Cochran 1967). Nonparametric procedures were used because of the nonnormal distribution of the data and high, unequal variances even after transformation. Differences between activities of males and females were evaluated with Mann-Whitney *U*-tests (Conover 1980). I evaluated differences in activities among the four time periods using Kruskall-Wallis tests with multiple-comparison statistics (Conover 1980).

RESULTS

Preflightless period.—Postbreeding scaup were first observed in mid-July. Numbers of postbreeding scaup gradually increased through the end of July as females terminated breeding efforts and males abandoned their mates (Table 1). These birds formed flocks of 2–65 birds by the last 2 weeks of July. Molt of body feathers was apparent in most males by the end of June and in females after mid-July (Austin and Fredrickson 1986). Observations of 15 marked birds indicated that individuals moved frequently among ponds during the day. At night, most postbreeding scaup roosted on the 2 largest lakes in the area (Otter Lake, 1115 ha; Proven Lake, 1012 ha). Several marked females were last seen in the area 3–7 days after losing their nests, and no marked birds were sighted during their flightless stage. These marked females that nested around Erickson probably molted elsewhere. Based on the loss of marked birds and the decline in the number of scaup present in the area (Austin 1983), it appeared that most birds that terminated breeding in July left the Erickson area by the end of July. The origin of scaup that molted in the Erickson area is unknown.

Males and females differed significantly in time invested in 3 of 6 activities. Females spent more time feeding than did males (34.4 and 29.8%, respectively; $P < 0.05$), whereas males spent more time swimming and in comfort activities than females (12.1 vs 8.9%, and 20.2 vs 18.1%, respectively; both $P < 0.05$). Scaup spent more time alert in the preflightless period than in the flightless or postflightless periods (both sexes, $P < 0.05$) (Fig. 1).

Flightless period.—Most scaup in postbreeding flocks were flightless by the second week of August and regained flight by early September. Flocks ranged in size from 25 to 55 birds and usually remained separate from other species and broods on the ponds.

Allocation of time among activities was not significantly different between sexes ($P > 0.05$) during the flightless period. Flightless birds spent less time feeding, swimming, and alert and spent more time resting than in either the preflightless or migratory period ($P < 0.05$). Time spent alert declined by more than 50% from the preflightless period. For males, time spent swimming declined and time spent resting increased ($P < 0.05$), similar to levels of females in this period. Comfort activities accounted

TABLE 1

PERCENT OF TIME SPENT IN VARIOUS ACTIVITIES BY POSTBREEDING LESSER SCAUP NEAR ERICKSON, MANITOBA, CANADA, 1982 (N = NUMBER OF OBSERVATION SESSIONS; M = MALES; F = FEMALES)

	Preflightless		Flightless		Postflightless		Migratory	
Period	M	F	M	F	M	F	M	F
N	22	32	11	11	35	42	40	40
Total h	57.8	65.6	21.6	23.6	79.0	99.3	79.7	79.7
Feed	29.8	34.4	28.2	29.3	25.8	28.3	45.0	42.6
Rest	22.5	27.0	37.1	36.6	40.9	37.7	21.5	20.3
Comfort	23.4	21.2	23.9	23.0	17.6	19.0	10.7	12.5
Swim	12.1	8.9	7.3	7.1	12.5	11.3	17.4	17.7
Fly	0.1	0.1	0	0	0.1	0.1	0.3	0.3
Alert	11.7	8.0	3.4	3.8	2.2	2.7	4.2	4.9

for a greater proportion of time in the flightless period than in any other period but was not significantly ($P > 0.05$) greater than in the preflightless period.

Postflightless period.—Numbers of scaup declined 72% over the postflightless period from the high of 148 birds in the flightless period. Observations of other ponds in the region also showed a similar decline in the numbers of adult scaup. Only fledged juveniles and scattered small groups of postflightless birds or late-molting females were present during this period. Flocks observed for time-budgeting ranged in size from 6 to 57 birds with smaller flocks, comprised predominantly of females, occurring in the last half of the period. Patterns of activity were similar between the sexes ($P > 0.05$). The levels of feeding and resting were similar to those in the flightless period. Time spent in comfort activities declined and swimming increased; however, differences were significant ($P < 0.05$) only for males. Time spent alert was lowest during this period.

Migratory period.—Initial appearances of staging and migratory scaup occurred in late September. Flocks roosted on Otter and Proven lakes at night and moved to smaller wetlands during the day. Flocks on ponds ranged in size from 30 to 600 birds during the migratory period. During the last 3 weeks before freeze-up, large flocks of more than 800 scaup remained on the largest lake during the day. Final departures from the area occurred approximately 3–7 days before the final freeze-up in early November.

Allocation of time among activities was similar between the sexes ($P > 0.05$). Feeding activity increased markedly ($P < 0.01$) from the postflight-

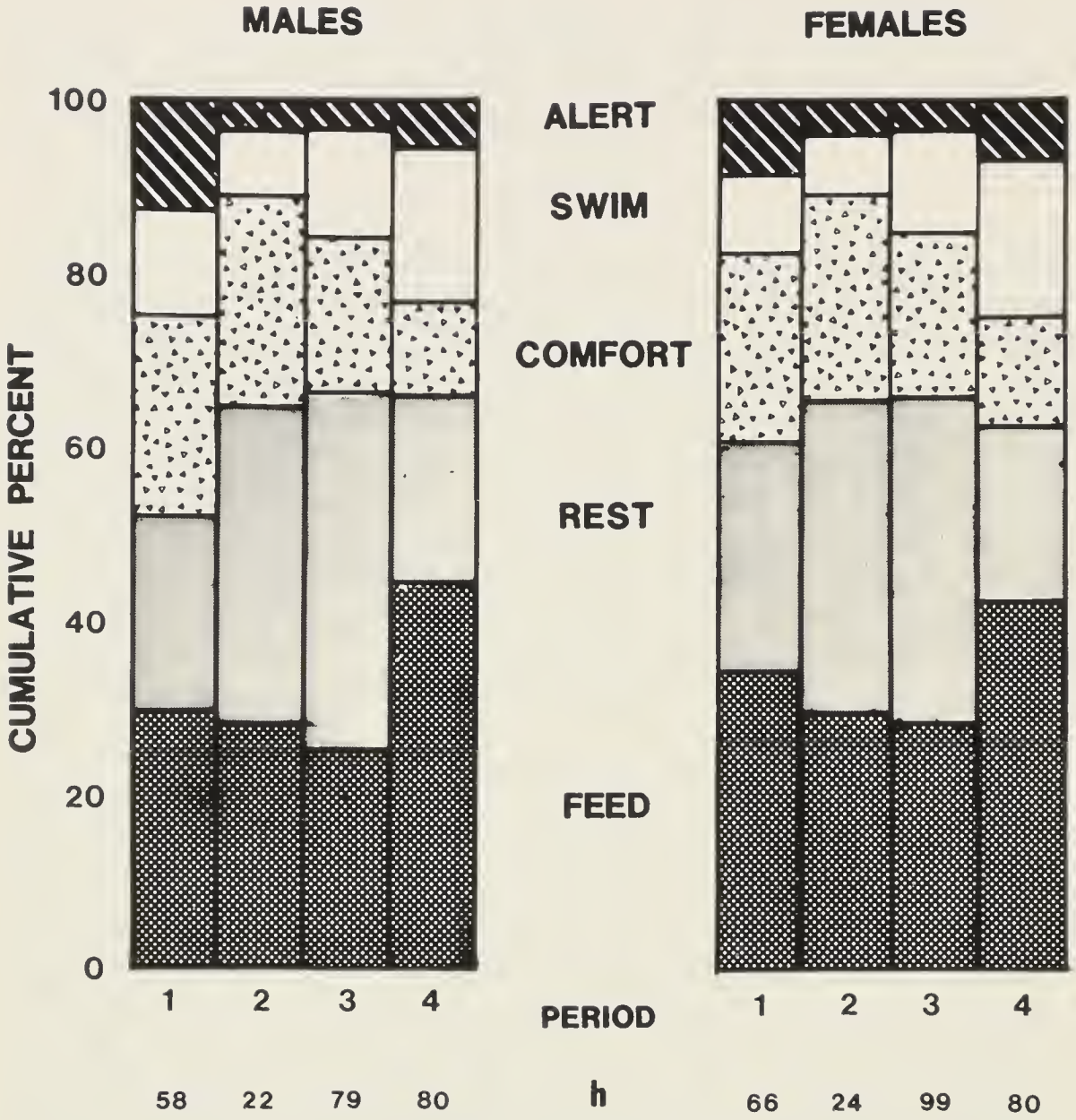

FIG. 1. Number of Lesser Scaup adults and broods present on 28 ponds near Erickson, Manitoba, Canada, 1982. Fledged juveniles were pooled with adults after September.

less period. Flocks were observed feeding intensively on ponds in the predawn hour after returning from the roost lakes; however, the low light conditions prohibited differentiation of the sexes and thus scan observations to quantify activities at these times. Swimming and flying activity also increased in this period ($P < 0.05$), whereas time devoted to comfort activities was lower ($P < 0.05$) than in all other periods.

DISCUSSION

The seasonal pattern of activities of postbreeding Lesser Scaup varied according to the stage of molt and the initiation of migration. Feeding

was low during and immediately after the wing molt and increased markedly during fall migration, corresponding to lipogenesis and increasing body weight in preparation for migration (Austin 1983). Time allocated to comfort activities, composed largely of preening, was positively related to the level of molt intensity. Molt intensity was greatest during the flightless and postflightless periods and declined markedly in migratory birds as molt was completed (Austin and Fredrickson 1986). Birds spent more time resting during the flightless period, when time allocated to feeding and alert were low; they spent the least time resting in the migratory period when feeding, flight, and alert activities were high. Scaup were most alert before both the molt and fall migration. Migratory restlessness before both the molt and fall migration is reflected in the greater time spent alert and swimming, particularly in fall. These activities have been reported in premigratory Redheads (*Aythya americana*) (Bailey 1982); captive Blue-winged Teal (*Anas discors*) (Owen 1968), and captive Gadwall (*Anas strepera*) (Oring 1969).

The differences in activities between sexes in the preflightless period may be due to the earlier onset of molt in males (Palmer 1976) and differences in body condition following the breeding season (Austin 1983). Plumage changes in males from alternate to the basic plumage were apparent in late June, whereas the first indication of molt in females occurred no earlier than mid-July (Austin and Fredrickson 1986). Thus molt in males during the preflightless period (July) is probably more advanced than in females, and the greater time spent preening by males may reflect this. Differences in time spent foraging in the preflightless period may be related to differences in body condition at the end of the breeding season. In Ring-necked Ducks (*Aythya collaris*), breeding males regained body weight and metabolic reserves in mid-June and July, whereas breeding females did not begin to regain body weight and reserves until mid-July (Hohman 1986). Body weights and metabolic reserves of female scaup were low in the period immediately following breeding (Austin 1983), and females spent significantly more time feeding than did preflightless males.

Allocation of time among activities in this study was compared with that in 2 other studies of Lesser Scaup conducted in southern Manitoba. Paired males staging on the Delta Marsh in spring spent 35% of their time foraging, or about 10% less time feeding than did males during fall migration (Siegfried 1974, based on individual birds; this study). Unpaired males in spring spent much more time resting (67%) and only 15% of their time foraging. Prebreeding female scaup spent about the same amount of time feeding as did migratory birds in fall, but they spent less time swimming and more time at rest. Although these females were prob-

ably undergoing the prebasic molt (Palmer 1976), time spent preening was less than half that in the preflightless and flightless periods (Siegfried 1974, this study). Brood females in the Erickson area allocated considerable time to the care of ducklings; a much higher percentage of time was spent alert (20.4%), and less time was spent feeding (17.6%) or resting (21.5%) than during the postbreeding period (Afton 1983, adjusted values; this study). In contrast, broodless females during this same time period also spent only 17.2% of their time feeding, but over 50% of their time resting. Afton's broodless females (known failed nesters) are probably equivalent to preflightless birds of this study, but his observations were most likely conducted earlier in their postbreeding or preflightless period than were my observations (A. Afton, pers. comm.) (e.g., immediately after the loss of the nest). Thus, based on the results from Afton (1983) and this study, preflightless females appear to spend twice as much time foraging as do brood females, and the time devoted to feeding increases later in the preflightless period.

The pattern of postbreeding activities for Lesser Scaup is similar to that of Redheads (Bailey 1982). Comparison between the two species, by sex, of time spent feeding and preening indicates a very similar pattern and amount of time for the period during and after the molt. Redheads fed primarily in the evening or at night and rested during the day. Night feeding and diurnal roosting have also been reported for captive molting Gadwall (Oring 1969). Whether scaup fed at night and on the large roost lakes is unknown. However, the low levels and absence of gain in body mass and fat levels in the flightless and postflightless periods (Austin 1983) suggests that the low diurnal feeding times are probably representative of the total time spent feeding.

The most marked differences between scaup and Redheads is in time allocated to alert and rest. Time spent alert by Redheads averaged <0.4%, whereas scaup spent 2.7–8.0% of their time alert. The greater alertness and less time spent resting may reflect the differences in habitat and disturbance factors between the two areas. Most small ponds in the Erickson area are adjacent to farmland, roads, or houses and, therefore, are more subject to human disturbances than secluded southern boreal lakes of Manitoba used by postbreeding Redheads in Bailey's study. Hunting activity also is probably higher in the Erickson area because of the area's proximity to population centers and because of better access to most ponds. Waterfowl traditionally molt in secluded areas, presumably to avoid disturbances during the flightless period when birds cannot move far and are vulnerable to disturbances or predation (Salomonsen 1968). The impact of human disturbances on time-budgets and habitat use patterns of scaup in the Erickson area is uncertain.

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ACTIVITY BUDGETS OF MALLARDS AND AMERICAN WIGEON WINTERING IN EAST-CENTRAL ALABAMA

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Abstract.—Mallards (*Anas platyrhynchos*) and American Wigeon (*A. americana*) were studied in Alabama from November through February 1983–85. Resting was the major activity of Mallards (39–54%) and feeding was the major activity of American Wigeon (45–71%). Mallards increased feeding during the colder winter of 1983–84, but wigeon did not. Locomotion (8–21% and 5–26%) and comfort (4–22% and 4–13%) also were dominant behavioral activities of Mallards and American Wigeon, respectively. Total time spent in alert, courtship, and agonistic behavior was low for both species (<11%). Mallards and wigeon rested most on river sites, while managed impoundments were used most for feeding and social activity. *Received 18 July 1986, accepted 27 Feb. 1987.*

Recent studies in North America have used activity budget techniques to investigate nonbreeding waterfowl ecology (e.g., Paulus 1984, Quinlan and Baldassarre 1984). Most investigations, however, spanned only one winter period and focused on one species. A multiple species approach can provide new ecological and behavioral insights (McKinney 1973) relative to nonbreeding waterfowl ecology, and studies longer than one year are necessary to determine the influence of annual effects on various aspects of wintering waterfowl behavior.

We studied activity budgets of Mallards (*Anas platyrhynchos*) and American Wigeon (*A. americana*) because these species are among the most abundant North American waterfowl (Bellrose 1980), yet little is known regarding their wintering ecology. Indeed, Fredrickson and Drobney (1979) noted the lack of data on nonbreeding waterfowl in general, and stressed the need to determine how species allocate time during this portion of the annual cycle. This is significant because events during winter may affect survival and subsequent reproductive performance of these and other waterfowl (Krapu 1981, Heitmeyer and Fredrickson 1981). Jorde et al. (1983, 1984) studied wintering Mallards using, in part, activity budget techniques. Their study site (Nebraska), however, was north of most major wintering areas (Bellrose 1980), and thus may not reflect winter activity of most North American Mallards. Wintering American Wigeon also have received little study except for work by Soutiere et al. (1972) and Wishart (1983a, b), which concentrated on pairing chronology and courtship behavior. Here we determine (1) the activity budgets of

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Mallards and American Wigeon wintering in Alabama, and (2) the influence of habitat selection and weather on activity.

STUDY AREA

Mallards and American Wigeon were observed at the 4520-ha Eufaula National Wildlife Refuge (NWR), which is located along both sides of the Alabama-Georgia border formed by the Chattahoochee River. Wetlands managed for waterfowl total 200 ha and include the Kennedy, Bradley, and the upper and lower Houston impoundments. Observation sites were the three habitat types of (1) the Chattahoochee River, (2) the upper Houston, and (3) the lower Houston.

River sites used by ducks were sandbars and islands characterized by sparse herbaceous and grassy growth, with woody growth on most higher elevations. The lower Houston impoundment is largely a deep (2–5 m), open water area dominated by watermilfoil (*Myriophyllum* spp.) and American lotus (*Nelumbo lutea*); emergent sites support arrowhead (*Sagittaria* spp.), swamp smartweed (*Polygonum hydropiperoides*), and pondweed (*Potamogeton* spp.) (Carroll 1983). Black willows (*Salix nigra*) occupy shallow margins of the unit. The upper Houston is shallower than the lower unit, but submergent vegetation is similar. Emergent vegetation is denser and dominated by smartweeds, American lotus, and spikerushes (*Eleocharis* spp.). Black willows also border this unit (Carroll 1983).

METHODS

Mallards and American Wigeon were observed from November through February 1983–84 and 1984–85. Observations were made from sunrise to sunset during three consecutive days/week. Birds were sampled in each of the three study habitats by drawing random numbers to assign a habitat to a day during the 3-day interval. Days then were divided into three equal time blocks, and time blocks into three equal time periods of approximately one-h. Two of the three periods were sampled within each time block by again randomly drawing numbers to assign Mallards or American Wigeon to a different period.

During a sampling period, two single (unpaired) males, two single females, and two pairs were selected by pointing a 60× spotting scope towards a flock and selecting the bird closest to the center of vision. Pair status was determined using criteria outlined by Hepp and Hair (1984). Individuals or pairs were observed from blinds or a parked vehicle for 10 min, and activities recorded into a tape recorder at 15-sec intervals (Wiens et al. 1970). Activities were defined as feeding, locomotion, resting, comfort, alert, courtship, agonistic, and out-of-sight (Paulus 1984). We obtained general climatic data from the weather station at Columbus, Georgia, 75 km north of the refuge (National Oceanic and Atmospheric Administration 1983–85).

Statistical analysis of percent time spent in each activity was performed after arcsine transformation of the nonnormal percentage data (Zar 1974). Activities during the diurnal cycle were compared by categorizing blocks as (1) early morning (periods 1–2), (2) midday (periods 3–7), and (3) late afternoon (periods 8–9). *t*-tests were conducted to determine differences in activity patterns between sexes and between pairs and singles within each month and year; data were pooled where not significant ($P > 0.05$) or significant with less than a three percent difference between means. Monthly activity patterns were determined for status groups (pairs vs singles) by averaging daily time spent in an activity, thus sample size is the number of days per month that birds in each status group were observed. Activity patterns by species within a habitat were determined by pooling status, years, and months. One-way analysis of variance and Duncan's multiple range test were used to determine

significant differences in activities ($P < 0.05$) among time blocks, months within years, and between species and habitat types. All statistical tests followed Steel and Torrie (1980).

RESULTS

Male vs female activity patterns.—A total of 907 Mallards and 751 American Wigeon was observed for 151 h and 125 h, respectively. Time spent in each activity was similar ($P > 0.05$) for paired and unpaired males and females of both species, except in 12 (2%) of 672 possible comparisons, therefore, data were combined for all further analyses.

Mallard activity patterns.—Resting was the most frequent ($P < 0.05$) activity of Mallards (39–54%) during all months except February 1984 (Fig. 1) and was usually the prevalent activity during each time block in the day. Mallard feeding increased throughout winter (Fig. 1), being lowest during November (7–10%), and highest in January and February, except for single birds in February 1985. Feeding was higher ($P < 0.05$) in December and February of 1983–84 vs 1984–85. Average monthly temperatures were similar ($P > 0.05$) between years, except that December 1983 was unusually cold ($\bar{x} = 7.6$°C) whereas December 1985 was warmer ($\bar{x} = 13.9$°C).

Total time spent in alert, courtship, and agonistic activities was highest in November 1984 (11%) and lowest in January 1984 (4%). Agonistic behavior was higher ($P < 0.05$) in December 1983 than in 1984. Courtship was similar among months in both seasons, but it was always higher ($P < 0.05$) for single compared to paired birds during December.

American Wigeon activity patterns.—There were no differences ($P > 0.05$) in activity of American Wigeon between paired and single birds or between months of different seasons (Fig. 1). Feeding usually dominated activity in all months (45–71%; $P < 0.05$) (Fig. 1), but was variable throughout the day (32–95%). Locomotion varied (0–50%) throughout the day and was lower ($P < 0.05$) in February than in January, when it peaked.

Total time spent in alert, courtship, and agonistic activities was low (<5%) during each month. Courtship activities comprised a small portion (0–1%) of the activity budget and did not differ among months within seasons ($P > 0.05$). Agonistic activities were similar among most months ($P > 0.05$), and low throughout the day for each status (<3%).

Activity patterns by habitat.—Feeding by both species usually was higher on impounded areas than on the river ($P < 0.05$) (Table 1). Time spent in locomotion was similar among habitats for each species, and between species within each habitat ($P > 0.05$). Resting by Mallards was higher ($P < 0.05$) on the lower vs the upper Houston where beaver dams, lodges, and downed trees furnished loafing areas.

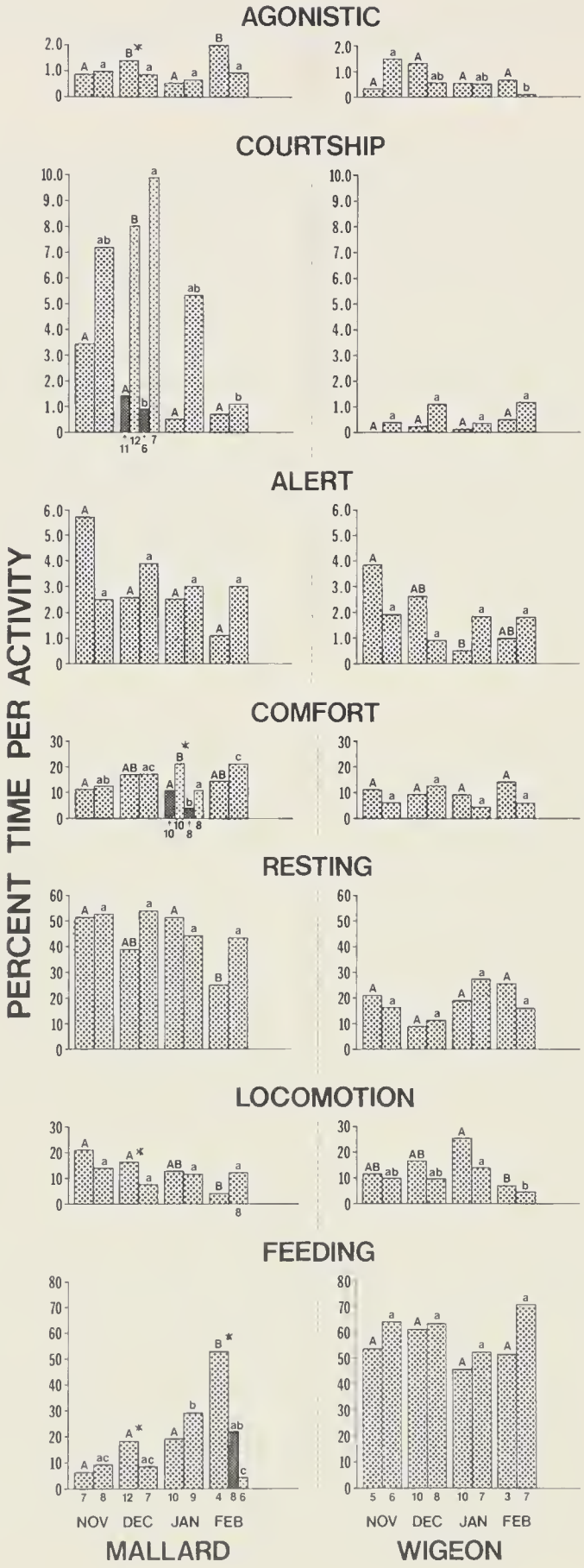
AGONISTIC
COURTSHIP
ALERT
COMFORT
RESTING
LOCOMOTION
FEEDING
PERCENT TIME PER ACTIVITY
NOV DEC JAN FEB
MALLARD
NOV DEC JAN FEB
WIGEON

TABLE 1

ACTIVITY PATTERNS WITHIN HABITAT TYPES FOR MALLARDS AND AMERICAN WIGEON WINTERING AT EUFAULA NWR, ALABAMA-GEORGIA

	Mallard			American Wigeon		
Activity	Lower (20)[a]	River (45)	Upper (18)	Lower (23)	River (28)	Upper (14)
Feeding	15.5[d]	17.5[d]	36.1[c]	63.2[b]	46.1[c]	72.0[b]
Locomotion	14.7[b]	12.7[b]	13.5[b]	17.9[b]	12.6[b]	10.7[b]
Resting	45.9[b]	48.8[b]	27.8[c]	10.2[d]	26.9[c]	6.7[d]
Comfort	10.2[b,c]	16.6[b]	11.4[b,c]	6.0[c,d]	12.4[b,c]	5.1[d]
Alert	5.8[b]	1.7[c]	3.3[b,c]	1.5[c]	1.3[c]	4.0[b]
Courtship	7.0[b,c]	1.8[c,d]	6.7[b]	0.5[d]	0.3[d]	0.6[d]
Agonistic	0.9[b,c]	0.9[b]	1.2[b]	0.9[b,c]	0.4[c]	0.9[b,c]

[a] Number of observation days.
[b,c,d] Means for each activity denoted by the same letters are not significantly different ($P > 0.05$).

DISCUSSION

The major difference in activity patterns between Mallards and American Wigeon at Eufaula NWR was the higher feeding and lower resting time of American Wigeon. Nonbreeding American Wigeon feed extensively on algae and leafy aquatic vegetation (Wishart 1983b), which were abundant on both study impoundments. Few American Wigeon were observed feeding in flooded cornfields or upland sites, and they probably spent more time feeding than did Mallards in order to obtain and process the lower quality natural foods that apparently dominated their diet at Eufaula NWR. Paulus (1982) noted that watermilfoil and algae are comparatively poor waterfowl foods and that species using them must feed extensively to meet nutritional needs.

Mallards may have spent less time feeding because they participated in evening feeding flights to flooded cornfields on the refuge. Corn provides an available, high energy food source that can increase foraging efficiency and minimize feeding time of Mallards and other ducks (Baldassarre and Bolen 1984). This reduced feeding time allows additional time for other activities such as resting.

←

FIG. 1. Seasonal activity patterns of Mallards and American Wigeon. For each species by activity, monthly comparisons that were not significantly different ($P > 0.05$) within seasons have identical letters above histobars (upper case = 1983–84, lower case = 1984–85). Within each month, differences between seasons are denoted by an asterisk. Significant status differences for each month within a year are noted by split histobars (solid = pairs, stippled = singles). Numbers below histobars denote sample size (number of observation days).

Increased feeding by Mallards during cold periods differs from reports of decreased feeding in response to colder temperatures in Nebraska (Jorde et al. 1984). Duration and severity of cold periods, however, render associated stresses more severe in northern versus southern areas, thus Mallards could use different strategies to maintain homeostasis. For example, waterfowl in northern areas often encounter inclement weather that renders natural foods unavailable (Jorde et al. 1983, Baldassarre and Bolen 1984). Mallards wintering farther south can still feed during cold weather because snow, and especially ice, seldom occur for long periods and inhibit food availability. Mallards may then increase feeding time rather than depend on accumulated lipid reserves.

Perhaps American Wigeon did not increase feeding in response to cold weather (i.e., December 1983 vs December 1984) because they could not meet increased metabolic demands by increasing already high feeding rates. American Wigeon may use stored body reserves as do other waterfowl during winter (Raveling 1979), or perhaps they select favorable microclimates at this time (Brodsky and Weatherhead 1984). Further research examining intraspecific geographical variation in lipid content and activity patterns is necessary to test this hypothesis.

Social activities comprised a small portion of overall time budgets of both species, but appeared important and possibly influenced by other flock activities. For example, increased alert time of paired Mallards in early mornings during December (9%) may be a response to higher courtship activities of single birds during this time (23%). Increased agonistic activity in December also may relate to courtship, or reflect increased aggressiveness as feeding time increased.

Differences in courtship activities during December appear influenced by pairing chronology and its effects on the ratio of paired and single birds. Pairing by Mallards occurs mainly from September through December, with 90% of individuals paired by January (Johnsgard 1960). Thus, increased courtship by single birds may reflect competition for fewer potential mates. Paired birds did not appear to court as frequently (Fig. 1), but remained in close association and occasionally engaged in displays and copulations. These activities may aid females in assessing breeding suitability of males or maintaining and strengthening pairbonds (Afton and Sayler 1982). Courtship activities by American Wigeon were lower possibly because only 60% are paired by mid-February (Soutiere et al. 1972).

Activity patterns by habitat.—Both species usually fed more on impoundments, which are managed for waterfowl, probably because these areas provided more natural food than did river sites. River sites, however, were used for resting and comfort because sandbars provided areas

for loafing and preening activities. Also, birds concentrated on southern and leeward sites, which appeared to maximize exposure to solar radiation and protection from northern winds.

Courtship was higher on impoundments perhaps because these areas provided habitat more suitable for pair formation. For example, the Houston impoundments, with higher structural diversity of vegetation, probably provided isolated areas, which can be important during pair formation (cf. Afton and Sayler 1982, Wishart 1983a).

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Wilson Bull., 99(3), 1987, pp. 465–467

SHORT COMMUNICATIONS

Size dimorphism in mated pairs of American Kestrels.—The degree of dimorphism between males and females has been examined in a number of raptors (Storer 1966, Reynolds 1972, Balgooyen 1976, Snyder and Wiley 1976), but few studies have reported the amount of dimorphism between mated pairs of birds. If the maintenance of a size difference within pairs is adaptive, then one would predict that selective mating would occur to minimize instances of overlap. American Kestrels (*Falco sparverius*) are only slightly dimorphic, with some overlap between the sexes (Brown and Amadon 1968). In captivity, American Kestrel pairs consisting of a small female and a large male were as productive as were pairs of large females and small males, leading Willoughby and Cade (1964) to conclude that large female size was not necessary for normal behavioral interactions or successful egg production. Whether such size variance occurs in naturally paired birds, however, is unknown. Here I report tarsal lengths and weights of mated pairs of wild American Kestrels and examine them for patterns of selective mating.

During 1982–1984 I studied mate replacement in American Kestrels in southwestern Quebec (Bowman and Bird 1986). In that study, I removed one member of a pair from each of 20 pairs of birds. Prior to the removal of a bird's mate, I trapped, banded, measured, and released the artificially widowed bird. Later its mate was also trapped and measured, and was kept in captivity until the end of the experiments. Females were trapped on the nest during the third week of incubation. Males were trapped with bow nets or with mist nets, using a live owl decoy, approximately 6–10 days after the trapping of their mates. Weights were taken to the nearest 0.1 g with a Pesola 300-g scale, and tarsal length was measured to the nearest 0.1 mm with Vernier calipers following the methods described by Bird and Lague (1982). I calculated a dimorphism index (DI_p) for each pair, using both tarsal length and the cube root of weight (Storer 1966).

I found that females were, on average, 28.6% heavier than their mates, and that they had 4.7% longer tarsi (Table 1). Although Balgooyen (1976) reported a mean female weight of 117.7 g (vs 147.1 g for this study), he did not state at which time of year females were weighed. Village (1983) reported that female Eurasian Kestrels (*F. tinnunculus*) gained weight before egg laying and maintained it through incubation. If this is true for American Kestrels, we should expect a higher mean weight for females during incubation.

Pair dimorphism indices for weight ranged from 1.3 to 15.5 (Table 1). Indices calculated from tarsal length ranged from −4.5 to 13.2 (Table 1), with 2 males having longer tarsi than their mates. The mean pair dimorphism index (DI_p) (Table 1) was similar to dimorphism indices for the entire sample (DI_s) based on the mean cube root of weight ($DI_s = 8.5$) and mean tarsal length ($DI_s = 4.6$). I found no correlation between male and female weight ($r_s = -0.227$, $P > 0.1$), nor between male and female tarsal length ($r_s = 0.269$, $P > 0.1$).

Female weight and tarsal length were correlated ($r_s = 0.552$, $P < 0.05$), but male weight and tarsal length were not ($r_s = 0.413$, $P > 0.05$), suggesting that male weight is not merely a function of body size. Female body weight during incubation is a function of male feeding efficiency (Newton 1979), thus females whose weight was greater than predicted by regression with tarsal length were assumed to have "quality" mates. I found no correlation, however, between male and female deviations from their predicted weight based on tarsal length ($r_s = -0.323$, $P > 0.05$), though the tendency was for heavy females to have lightweight mates. This suggests the possibility of either assortative mating or variation in male feeding effort. Female deviation from predicted weight was not correlated with the pair dimorphism index

TABLE 1

WEIGHT, TARSAL LENGTH, AND DIMORPHISM INDICES (DI_p)[a] FOR MATED PAIRS OF AMERICAN KESTRELS

	Weight (g)			Tarsal length (mm)		
Pair no.	Male	Female	DI_p	Male	Female	DI_p
1	126	145	4.7	41.9	41.4	−1.2
2	114	167	12.7	38.2	43.6	13.2
3	121	145	6.0	39.3	43.2	9.5
4	126	131	1.3	37.0	39.4	6.3
5	118	159	9.9	38.7	41.3	6.5
6	106	167	15.1	38.1	40.3	5.6
7	108	146	10.0	38.2	39.9	4.4
8	116	130	3.8	38.7	38.9	0.5
9	117	149	8.1	38.1	40.1	5.1
10	112	139	7.2	38.5	39.4	2.3
11	121	149	6.9	39.0	40.7	4.3
12	101	150	13.2	38.0	41.2	8.1
13	120	151	7.7	39.2	41.1	4.7
14	94	150	15.5	38.6	39.9	3.3
15	111	132	5.8	38.0	30.0	2.6
16	120	140	5.1	39.1	40.1	2.5
17	109	141	8.6	38.1	40.1	5.1
18	121	140	5.1	38.6	39.1	1.3
19	119	160	9.9	37.4	40.2	7.2
20	108	151	11.2	38.5	36.8	−4.5
$\bar{x}$ =	114.4	147.1	8.4	38.5	40.3	4.3
SD =	8.2	10.6	3.8	1.00	2.10	3.9

[a] DI_p = 100(female parameter − male parameter)/0.5(female parameter + male parameter). Modified from Storer (1966).

based on tarsal length ($r_s = 0.243$, $P > 0.05$), as would be expected if assortative mating was occurring. Female deviation from predicted weight was, however, significantly correlated with the dimorphism index based on weight ($r_s = 0.768$, $P < 0.01$); suggesting that as male feeding effort increases female weight increases and male weight decreases. As male feeding effort varies, we should not expect a correlation between tarsal length and weight in male kestrels during incubation.

Storer (1966) and Amadon (1975) reported that the more insectivorous races of American Kestrels were less dimorphic than the more rodent-eating races. Among 3 subspecies, *F. s. sparverius* is the most dimorphic. However, at least in tarsal length, my data show that some size overlap exists within mated pairs. My results suggest that kestrels are pairing randomly with respect to these characters. Kemp (1987) found a large degree of overlap between mated pairs of Greater Kestrels (*F. rupidcoloides*) suggesting no assortative mating in this slightly dimorphic species. European Sparrowhawks (*Accipiter nisus*) paired randomly with respect to wing length (Newton et al. 1983).

Most theoretical discussions of reversed size dimorphism (RSD) assume that it is an adaptive character associated with a raptorial lifestyle (Snyder and Wiley 1976). Recently, Mueller (1986) suggested that RSD can evolve only through sexual selection, and that

appreciable RSD can evolve only if there is selection both for large females and for small males. One prediction of this hypothesis is that in species in which sexual size overlap occurs, assortative mating should also occur. My data fail to support this hypothesis in American Kestrels. Additional research comparing assortative mating patterns, pair dimorphism, and reproductive success is needed to test Mueller's hypothesis further.

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Did the 1982–1983 El Niño-Southern Oscillation affect seabirds in Alaska?—The causes and effects of the oceanographic and atmospheric phenomena known as El Niño and the Southern Oscillation (ENSO) have been studied intensively in recent years (Cane 1983, Rasmusson and Wallace 1983, Barber and Chavez 1983, Cane and Zebiak 1985). ENSOs occur at semiregular intervals of 3–4 years, and the stronger events have important biological consequences, including reduced breeding success and survival of seabirds in the central and eastern tropical Pacific (Boersma 1978, Barber and Chavez 1983, Schreiber and Schreiber 1984, Duffy 1986). The ENSO event of 1982–1983 was perhaps the strongest of this century (Cane 1983), and there is evidence that seabird populations as far north as the Oregon coast (42–46°N) were adversely affected (Hodder and Graybill 1985, Bayer 1986). Here I examine evidence for similar effects on seabirds along the Alaskan coast.

In 1983 there was widespread breeding failure among some surface-feeding seabirds in the Gulf of Alaska and eastern Bering Sea. The phenomenon seemed to be most pronounced in the Black-legged Kittiwake (*Rissa tridactyla*). Essentially, total breeding failure occurred at four kittiwake colonies visited in the Gulf of Alaska (Fig. 1) (Table 1), and at two colonies in the Bering Sea (Table 2). A few young were raised at a colony in Norton Sound, however, and production appeared to be about average at Cape Lisburne in the Chukchi Sea.

In addition to the observed breeding failure, there was widespread mortality of adult Black-legged Kittiwakes and Short-tailed Shearwaters (*Puffinus tenuirostris*) in Alaskan waters during August and September 1983 (D. R. Nysewander and J. L. Trapp, unpubl. data).

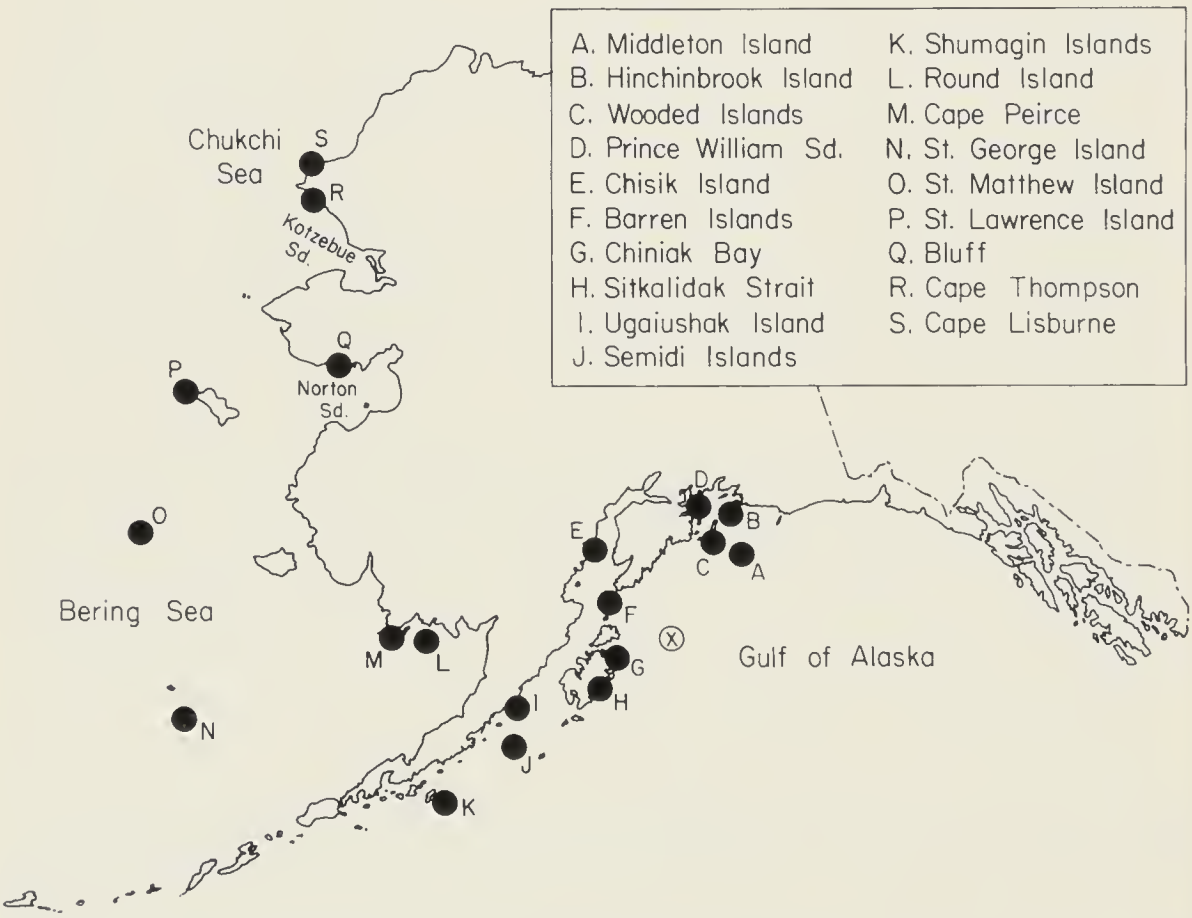

FIG. 1. Locations of Black-legged Kittiwake colonies studied in Alaska between 1976 and 1985. The circled "X" denotes the location in the Gulf of Alaska for which sea surface temperature data are plotted in Figure 2.

TABLE 1

NUMBER OF YOUNG PER PAIR FOR BLACK-LEGGED KITTIWAKES AT COLONIES IN THE GULF OF ALASKA, 1976–1985 (MISSING VALUES INDICATE NO DATA)[a]

Location	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	$\bar{x}$	N
Middleton[b]	—	—	0.14	—	—	≥0.47	0.30	0.03	0.67	0	0.27	6
Hinchinbrook[c]	≤0.03	≤0.51	≤0.04	—	—	—	—	—	0.28	—	0.22	4
Wooded Is.	0.33	0.63	—	—	—	—	—	—	—	—	0.48	2
Prince Wm. Sound[c]	—	—	—	—	—	—	—	—	0.31	0.15	0.23	2
Chisik[d]	—	—	0.01	0.36	—	—	—	0	—	—	0.12	3
Barren Is.[e]	—	0.08	0.14	—	—	—	—	—	—	0	0.07	3
Chiniak Bay[f]	—	1.23	0.61	—	—	—	—	0	0.42	0	0.45	5
Sitkalidak	—	0.74	0.17	—	—	—	—	—	—	—	0.46	2
Ugaiushak	0.07	0.77	—	—	—	—	—	—	—	—	0.42	2
Semidi Is.[g]	0.29	0.62	0	0.36	0.30	1.04	—	0	—	0	0.33	8
Shumagin Is.[h]	0.60	—	—	—	—	—	—	—	—	0	0.30	2
$\bar{x}$	0.26	0.65	0.16	0.36	0.30	0.76	0.30	0.01	0.42	0.03	0.30	
N	5	7	7	2	1	2	1	4	4	6		39

[a] All data for 1976–1978 included in Baird et al. (in press). Other sources as noted below.
[b] P. J. Gould, D. R. Nysewander, B. Roberts (pers. comm.).
[c] D. B. Irons (pers. comm.).
[d] R. D. Jones, M. R. Petersen, G. Mulberg (pers. comm.).
[e] S. A. Hatch (unpubl. data).
[f] L. D. Krasnow, D. R. Nysewander (pers. comm.).
[g] S. A. Hatch (unpubl. data).
[h] E. P. Bailey (pers. comm.).

TABLE 2

NUMBER OF YOUNG PER PAIR FOR BLACK-LEGGED KITTIWAKES AT COLONIES IN THE EASTERN BERING AND CHUKCHI SEAS, 1976–1985 (MISSING VALUES INDICATE NO DATA)

Location	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	$\bar{x}$	N
Round Island[a]	—	—	—	—	—	—	—	—	—	0	0	1
Cape Peirce[b]	0.25	0	—	—	—	0.16	—	—	0.01	0	0.08	5
St. George[c]	0.62	0.45	0.22	0.40	0.38	0.07	0.01	0.01	0.14	0.12	0.24	10
St. Matthew[d]	—	—	—	—	—	—	0	0	—	0.19	0.06	3
St. Lawrence[e]	0	—	—	—	—	0.86	—	—	—	—	0.43	2
Bluff[f]	0.04	0.11	0.82	1.05	0.85	0.91		0.29	0	0	0.45	9
Cape Thompson[g]	0	0.50	0.50	1.10	—	—	1.15	—	—	—	0.65	5
Cape Lisburne[h]	0.14	0.61	0.78	1.70	1.53	1.36	—	0.61	0	0.20	0.77	9
$\bar{x}$	0.18	0.33	0.57	1.06	0.91	0.67	0.39	0.23	0.04	0.09	0.41	
N	6	5	4	4	3	5	3	4	4	6		44

[a] J. Sherburne (pers. comm.).
[b] Lloyd (1985, pers. comm.). M. R. Petersen (pers. comm.).
[c] Hunt et al. (1981). Lloyd (1985). G. V. Byrd (pers. comm.).
[d] Springer et al. (1985a). E. C. Murphy (pers. comm.).
[e] Searing (1977). Springer et al. (1985b).
[f] Drury et al. (1981). E. C. Murphy (pers. comm.).
[g] Springer et al. (1985c).
[h] Springer et al. (1985b), G. V. Byrd (pers. comm.).

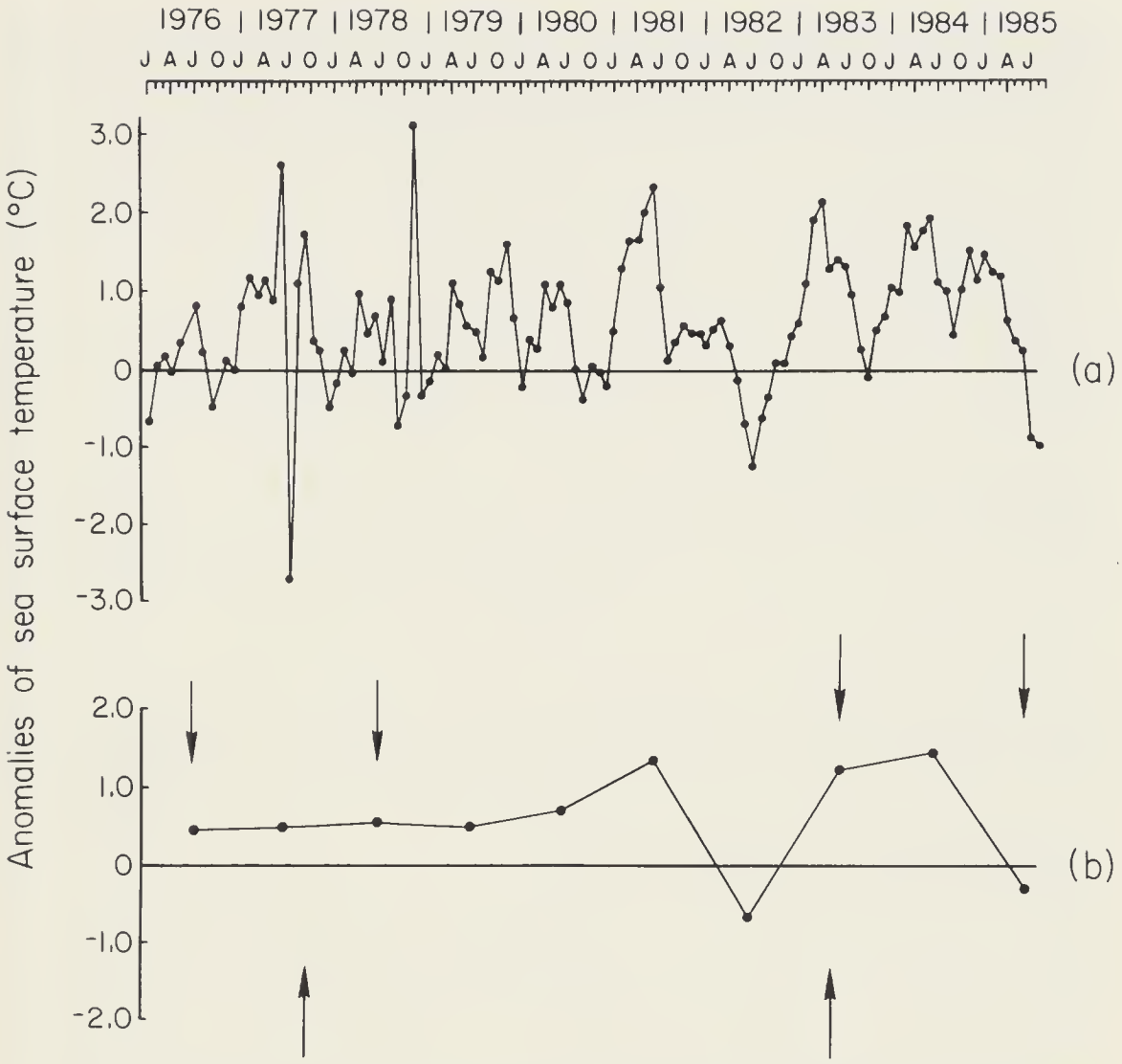

FIG. 2. Sea surface temperatures recorded near Kodiak (58°00′N, 150°00′W) expressed as deviations from the long-term mean: (a) mean monthly deviations, 1976–1985; (b) 4-month mean deviations during the seabird breeding season, May–August. Upper arrows indicate years of widespread breeding failure of kittiwakes in Alaska. Lower arrows show the timing of two major El Niño events in the southern hemisphere. Temperature data for 1976 to 1980 are from the Navy Fleet Numerical Oceanography Center, Monterey, California (courtesy D. R. McLain); data for 1981–1985 are from the Oceanographic Monthly Summary (National Oceanic and Atmospheric Administration, Washington, D.C.).

Large numbers of birds were found dead or dying, apparently from starvation, on beaches from the central Gulf of Alaska to Kotzebue Sound on the northwest coast.

Water temperatures in the Gulf of Alaska were above normal beginning in December 1982 and reached positive anomalies of 2°C or more during the spring and summer of 1983 (Royer and Xiong 1984, Xiong and Royer 1984) (Fig. 2). Niebauer (1980, 1983, 1984) has found significant correlations of air and sea temperatures in the Bering Sea with some large-scale atmospheric fluctuations, including the Southern Oscillation.

When viewed out of context, the above observations suggest an effect of the 1982–1983 ENSO on seabirds in Alaska. The inference, however, must be put in perspective by noting

that poor production of kittiwakes has occurred repeatedly in Alaska since at least 1976, with no clear relationship to major ENSO events. Overall, the annual production of kittiwakes in Alaska is low (compared with colonies in the northeastern Atlantic; Coulson and Porter 1985, Coulson and Thomas 1985), and failure of a colony to produce any young in a given year is common. If we define a colony failure as any instance of less than 0.1 young per pair being produced in a colony, there have been 15 such failures (38%) in 39 colony-years of observations in the Gulf of Alaska and 15 (34%) failures in 44 colony-years of study in the Bering and Chukchi Seas (Tables 1 and 2).

Although breeding failure was reported for at least one locality in all years except 1979 and 1980, it was especially prevalent in four years during the last decade: 1976, 1978, 1983, and 1985. Colonies in the Gulf of Alaska and Bering and Chukchi seas were affected in 1976, whereas the 1978 failure was largely confined to the Gulf. The 1983 and 1985 events involved colonies throughout Alaska, although the northernmost colonies seem to have fared somewhat better in both years.

The observation of higher than normal sea surface temperatures in 1983 must also be considered in context. Summer surface temperatures in the Gulf of Alaska have tended to be higher than the climatological mean during the last 10 years, and they were subject to wide annual variation during the last 5 years (Fig. 2B). Near Kodiak, the positive anomalies in 1983 were no greater than during the same periods in 1981 and 1984; years when kittiwake production was relatively good. Furthermore, production was extremely poor in 1985 (possibly worse than in 1983), when water temperatures were slightly cooler than normal. The failures of 1976 and 1978 were not obviously associated with changes in surface conditions, as the 1976–1977 El Niño produced no discernible signal in summer surface temperatures near Kodiak. Thus there has been no consistent relationship of kittiwake productivity to sea surface temperature in the Gulf of Alaska.

The environmental correlates of breeding failure are clearer, perhaps, in the colder seas north of the Alaska Peninsula and Aleutian Islands, but the relationships there are not consistent among areas. For instance, warmer springs in Norton Sound and the Chukchi Sea seem to promote successful breeding (Springer et al. 1985b), whereas colder temperatures favor breeding in the southeastern Bering Sea (Lloyd 1985). The evidence casts much doubt whether any single environmental factor will prove to be a good predictor of seabird breeding success in different years or regions.

Against this background, the widespread breeding failure of kittiwakes in 1983 cannot be taken as strong evidence of El Niño effects in Alaska. More compelling perhaps was the large die-off of adults that occurred in late summer and fall that year. The number of birds involved was not determined, but crude estimates ranged from tens of thousands to hundreds of thousands of dying seabirds (Nysewander and Trapp, pers. comm.). In addition to the two species most affected (Black-legged Kittiwakes, Short-tailed Shearwaters), lesser numbers of Northern Fulmars (*Fulmarus glacialis*), Glaucous-winged Gulls (*Larus glaucescens*), Pelagic Cormorants (*Phalacrocorax pelagicus*), and other species appeared on beaches. All carcasses examined were greatly emaciated, suggesting that starvation was the primary cause of death. The magnitude of summer mortality in 1983 appears to be unprecedented in recent years; A. L. Sowls (pers. comm.) reported that adult kittiwakes were again dying in considerable numbers near St. Matthew Island, Bering Sea, in July 1984.

The marked annual variation of kittiwake productivity and survival in Alaska may result from this species' specialized summer diet (Sanger, in press) and its limitation to surface feeding. The productivity of Northern Fulmars, a more omnivorous surface-feeder, has closely paralleled that of kittiwakes since 1976, but the annual fluctuations tend to be smaller (Hatch 1985). The annual production of diving seabirds, moreover, appears to bear little

relationship to that of the surface feeders, despite wide overlap in summer diets. For instance, in both 1983 and 1985, Common Murres (*Uria aalge*), Thick-billed Murres (*U. lomvia*), and puffins (*Fratercula* spp.) had good to excellent breeding success at the Semidi Islands; 1983 was in fact the most productive year for Horned Puffins (*F. corniculata*) of the six years studied since 1976 (Hatch, unpubl. data). Thus, environmental effects on seabird productivity in Alaska appear to differ among species with different foraging styles.

To summarize, the occurrence of widespread adult mortality in summer suggests an effect of ENSO on Alaskan seabirds in 1983. However, an overview of breeding performance in recent years reveals that: (a) some subsurface-foraging seabirds were unaffected during the 1983 event, (b) annual variation in the breeding success of one surface-foraging species has shown no consistent relationship to warm-water anomalies in the Gulf of Alaska, and (c) there may be marked regional differences in the effect of a given set of oceanographic conditions. These points are all in need of further understanding before the question of ENSO effects on high latitude seabirds can be resolved with confidence.

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Postbreeding movements of selected species of birds in Athens, Georgia.—During the postbreeding period individuals of many species leave their breeding habitats to wander considerable distances. This period is, perhaps, the least known and understood portion of the avian life cycle (cf. Greenwood and Harvey 1982). This paucity of data is understandable because in many cases birds stop singing, and become secretive, or leave the study area completely, making study difficult. Here we report on the postbreeding movements of several passerine species at a north Georgia study site.

Study area.—The study was conducted at the Horseshoe Bend Research Area in Athens, Clarke County, Georgia, in the Piedmont region 90 km south of the Appalachian highlands. The topography is gently rolling with slopes generally less than 15° (R. H. Delia and C. M. Morgan, pers. comm.). Climate is mild with a mean daily temperature of 24.5°C in June and average annual rainfall of 127 cm. The site is roughly 13 ha, bounded on 3 sides by the North Oconee River and on the fourth side by a 4-lane highway. It contains both riparian forest and old field habitats (Fig. 1).

Riparian forest comprises a strip 50–100 m in width bordering the river, in which elm (*Ulmus americana*) and red maple (*Acer rubrum*) are the dominant overstory species. Canopy height is 15–20 m. The old field community, which is isolated from other similar habitat by a minimum of 150 m (Fig. 1), is dense herbaceous growth (e.g., *Aster, Ambrosia,* and *Cassia*), 1–2 m in height, with emergent saplings (*Acer, Ligustrum*) 2–3 m in height taking over parts of the site.

Methods.—Sixteen nylon mist nets (12 m × 2.6 m × 30 mm, 36 mm, and 61 mm mesh) were placed 50 m apart in the forest along a path that roughly paralleled the river (Fig. 1). Seven of these nets were placed on 17 April, 2 on 3 May, and 7 on 10 May. On 16 July, 7 additional nets were placed 50 m apart on a curved line through the old field. Nets were usually run from daybreak until 12:00. Birds were trapped from 17 April to 15 October 1980. All were banded with U.S. Fish and Wildlife Service bands. Date, time, net number, molt, and fat were recorded for each capture. Sex was determined whenever possible by plumage, brood patch, or cloacal protuberance. Age was determined by examination of plumage and degree of skull pneumatization. The amount of subcutaneous fat was characterized as none = no fat in furcular region; very light = traces of fat in the furcular region; light = furcular region filled with fat, traces in the axillary region; moderate = furcular and axillary regions covered with fat, traces in abdominal region; and heavy = abdomen covered with fat. Molt was characterized as none = no pin feathers or sheathing in any tract, light = 1–4 in a given tract, moderate = 5–9, and heavy = 10 or more. Daily notes were kept throughout the study on species observed or heard singing on the site.

Results and discussion.—We captured 374 birds of 55 different species during 4733 net-h. Based on individuals heard singing, nests observed, or observations of young being fed in addition to capture data, we concluded that a minimum of 17 species bred on the Horseshoe Bend study site in 1980 (Table 1). Another 21 species were captured in spring or fall (Table 1). A third group of species does not fit into either of these categories. These birds are known to breed in the state of Georgia, but there was no evidence of their presence on the old field portion of the site until they were captured there in July and August (Table 2). Some of these species are known to breed commonly in the Athens area, but for others there are few or no records as breeding birds in the area.

Thirty-three individuals of 14 species (Table 2) exemplify postbreeding movement. When captured at our old field site, they were either out of their normal habitat, out of their breeding range, or not known to have been nesting on our specific site based on netting and observations.

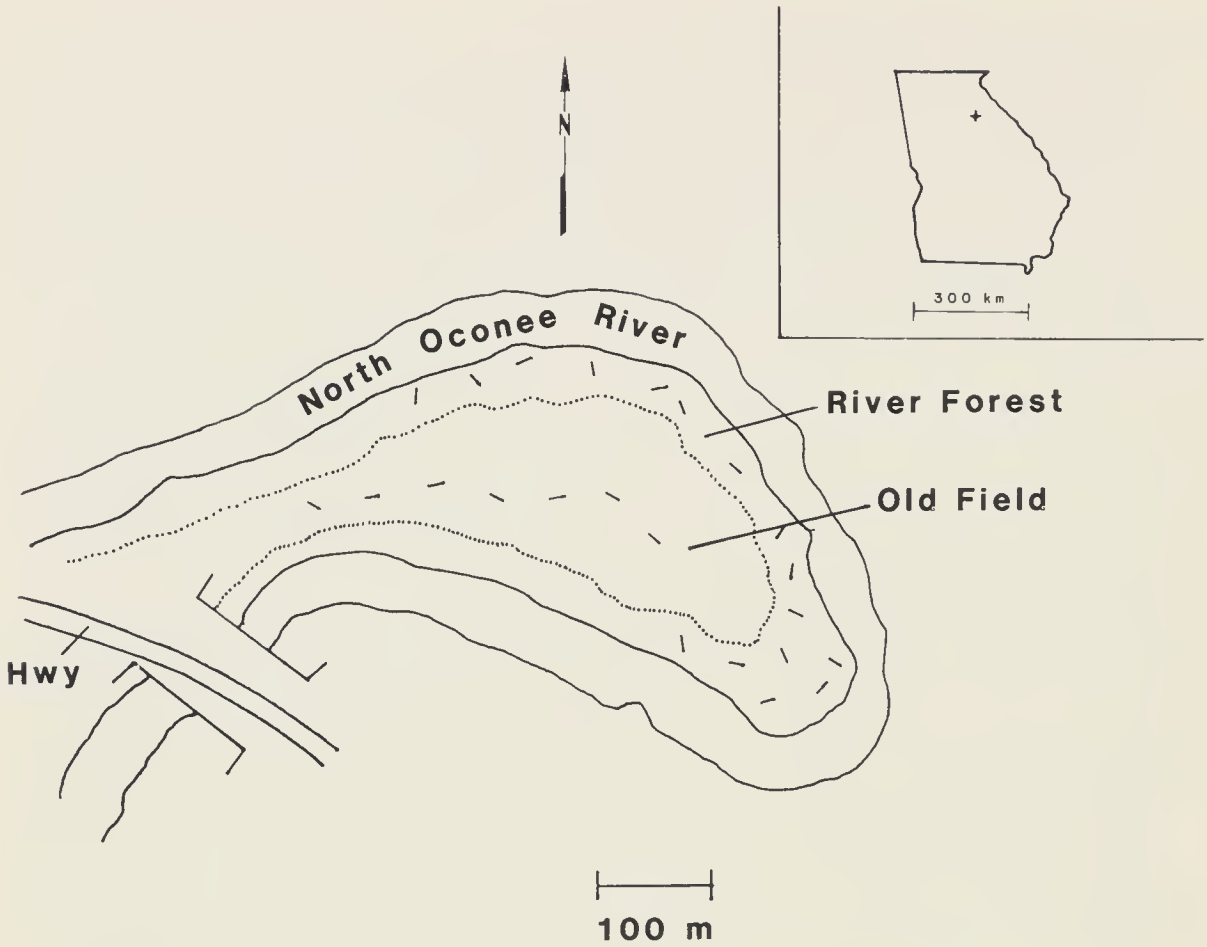

FIG. 1. Location of the river forest and old field study sites at Horseshoe Bend study area. Dashes (–) represent net locations.

We distinguish 4 subgroups based on habitat preferences, breeding range, and seasonal status in Athens (Burleigh 1938, Johnston 1954, Tramer 1968):

Species breeding on the site but not in the old field.—The Wood Thrush (scientific names are in Table 1), the only bird in this category, was a common breeding species in the riparian forest portion of the study area where singing individuals were heard from the beginning of the study (17 April) until 15 July. Although 33 Wood Thrushes were captured in the forest, no Wood Thrush was seen, heard, or captured in old field habitat until 21 July. Thereafter, 4 of these birds were captured in old field habitat during July and August. Two of the 4 individuals showed moderate or heavy molt, little or no fat, and had been eating pokeberries (*Phytolacca americana*). No Wood Thrushes were captured in riparian forest from 30 July until 17 September.

Species breeding in the Athens area in old field habitat, but not found as breeders on our site.—Five species (Yellow-billed Cuckoo, Ruby-throated Hummingbird, Brown Thrasher, Prairie Warbler, and Blue Grosbeak) met these criteria.

Species breeding in the Athens area, but not in old field type habitats.—Two species (Acadian Flycatcher [riparian forest] and Pine Warbler [mature pine forest]) met these criteria.

Species breeding commonly in the north Georgia mountains that are rare or absent as breeders in the Athens area.—Six species (Northern Parula, Black-and-white Warbler, American Redstart, Ovenbird, Canada Warbler, and Scarlet Tanager) met these criteria.

TABLE 1

BREEDING BIRDS, TRANSIENTS, AND WINTER RESIDENTS CAPTURED AT THE HORSESHOE BEND STUDY SITE

Species	Status[a]	Habitat[b]	Captures	Recaptures
Sharp-shinned Hawk (*Accipiter striatus*)	WR	RF	1	0
Northern Bobwhite (*Colinus virginianus*)	PR(B)	OF	1	0
Eastern Screech-Owl (*Otus asio*)	PR(B)	RF	2	0
Northern Flicker (*Colaptes auratus*)	WR	RF	1	0
Downy Woodpecker (*Picoides pubescens*)	PR(B)	RF	2	2
Pileated Woodpecker (*Dryocopus pileatus*)	PR(B)	RF	2	0
Great Crested Flycatcher (*Myiarchus crinitus*)	T	RF	1	0
Eastern Wood-Pewee (*Contopus virens*)	T	RF	1	0
Blue Jay (*Cyanocitta cristata*)	PR(B)	RF	14	2
Carolina Chickadee (*Parus carolinensis*)	PR(B)	RF	4	0
Tufted Titmouse (*P. bicolor*)	PR(B)	RF	17	3
Carolina Wren (*Thryothorus ludovicianus*)	PR(B)	RF	29	10
House Wren (*Troglodytes aedon*)	WR	RF	1	0
Veery (*Catharus fuscescens*)	T	RF	4	0
Gray-cheeked Thrush (*C. minimus*)	T	RF	1	0
Swainson's Thrush (*C. ustulatus*)	T	RF	5	0
Wood Thrush (*Hylocichla mustelina*)	SR(B)	RF	33	17
American Robin (*Turdus migratorius*)	WR	RF	5	0
Gray Catbird (*Dumetella carolinensis*)	SR(B)	OF	22	6
White-eyed Vireo (*Vireo griseus*)	SR(B)	OF	13	6
Yellow-throated Vireo (*V. flavifrons*)	T	RF	1	0
Red-eyed Vireo (*V. olivaceus*)	T	RF	5	0
Blue-winged Warbler (*Vermivora pinus*)	T	OF	1	0
Golden-winged Warbler (*V. chrysoptera*)	T	OF	1	0
Yellow Warbler (*Dendroica petechia*)	T	OF	1	0
Chestnut-sided Warbler (*D. penyslvanica*)	T	OF	2	0
Magnolia Warbler (*D. magnolia*)	T	OF	5	0
Yellow-rumped Warbler (*D. coronata*)	T	OF	5	0
Worm-eating Warbler (*Helmitheros vermivorus*)	T	RF	1	0
Kentucky Warbler (*Oporornis formosus*)	T	OF	3	0
Common Yellowthroat (*Geothlypis trichas*)	SR(B)	OF	29	0
Hooded Warbler (*Wilsonia citrina*)	T	OF	4	0
Yellow-breasted Chat (*Icteria virens*)	SR(B)	OF	1	0
Northern Cardinal (*Cardinalis cardinalis*)	PR(B)	RF, OF	27	3
Indigo Bunting (*Passerina cyanea*)	SR(B)	OF	6	0
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	PR(B)	RF	4	0
Field Sparrow (*Spizella pusilla*)	PR(B)	OF	4	0
White-throated Sparrow (*Zonotrichia albicollis*)	WR	RF	7	0

[a] PR = permanent resident; SR = summer resident; WR = winter resident; T = transient; (B) = breeds on the site.
[b] RF = riparian forest; OF = old field.

Table 2

Postbreeding Wanderers Captured during July and August 1980 in Old Field Habitat of the Horseshoe Bend Study Area

Species	Capture date	Sex[a]	Age[b]	Fat[c]	Molt[d]
Yellow-billed Cuckoo					
(*Coccyzus americanus*)	5 Aug	U	U	Very light	None
Ruby-throated Hummingbird	23 Jul	U	U	None	Heavy breast
(*Archilochus colubris*)	1 Aug	F	A	None	None
	12 Aug	U	U	Very light	Moderate breast
	31 Aug	M	A	None	Moderate body
Acadian Flycatcher	12 Aug	F	I	Very light	Moderate body
(*Empidonax virescens*)	14 Aug	U	A	Very light	Light body
	18 Aug	U	A	Very light	Light body
	18 Aug	U	A	Very light	Light body
	19 Aug	U	I	Very light	Light body
Wood Thrush	21 Jul	U	U	None	None
(*Hylocichla mustelina*)	21 Jul	F	A	Very light	None
	19 Aug	U	I	Light	Heavy body
	28 Aug	U	I	None	Moderate body
Brown Thrasher					
(*Toxostoma rufum*)	17 Jul	F	A	None	None
Northern Parula	21 Jul	U	I	None	Heavy body
(*Parula americana*)	21 Jul	U	I	None	Heavy body
	30 Jul	M	A	None	Heavy body
	8 Aug	U	I	Very light	None
	12 Aug	U	I	Very light	Heavy body
Pine Warbler					
(*Dendroica pinus*)	18 Aug	U	I	Very light	None
Prairie Warbler	26 Jul	U	I	Very light	None
(*D. discolor*)	14 Aug	F	A	Very light	Light breast
Black-and-white Warbler	17 Jul	U	U	U	U
(*Mniotilta varia*)	31 Aug	F	I	Light	None
American Redstart					
(*Setophaga ruticilla*)	8 Aug	F	A	Very light	Light body
Ovenbird					
(*Seiurus aurocapillus*)	25 Jul	F	A	None	Heavy body
Canada Warbler					
(*Wilsonia canadensis*)	8 Aug	M	I	Heavy	None
Scarlet Tanager					
(*Piranga olivacea*)	21 Aug	F	U	Heavy	Moderate body
Blue Grosbeak					
(*Guiraca caerulea*)	14 Aug	F	A	Very light	Light breast
	28 Aug	U	I	Very light	None
	28 Aug	U	I	Very light	None
	28 Aug	U	I	Very light	None

[a] F = female, M = male, U = unknown.
[b] J = juvenile, A = adult, U = unknown.
[c] See text for fat class descriptions.
[d] See text for molt class descriptions; "body" = molt found in all tracts, except wings and tail.

Although postbreeding movement has often been equated with the beginning of fall migration (Bent 1953, Hahn 1937, Pulich 1976), over half (19 of 33) of the postbreeding wanderers we trapped showed some degree of molt. Though individuals of several species do overlap molt and migration somewhat, such birds usually represent a small percentage of the population (Rappole, unpubl. data). Furthermore, few individuals of any species show heavy body molt during migration, a condition found in 7 of the birds captured in the old field habitat (1 Ruby-throated Hummingbird, 3 Wood Thrushes, 2 Parula Warblers, 1 Ovenbird).

The lack of subcutaneous fat reserves also argues against these birds being in a migratory state. Only 2 of the 33 birds captured, a Canada Warbler and a Scarlet Tanager, showed more than light fat reserves. Also, 5 of the species (Wood Thrush, Brown Thrasher, Ovenbird, Canada Warbler, and Scarlet Tanager) were captured at the site long before early migration dates for the species in north Florida, based on 25 years of TV tower kill data (Crawford 1981).

A southward "drift" is indicated by the fact that several of the species captured breed commonly 100 km or so north of the study area (Burleigh 1958, Denton et al. 1977) but are rare or absent as breeders in Athens or farther south (Burleigh 1958). To call this a migration, however, is not warranted, given the lack of fat reserves and the presence of molt in many cases. Such a drift has been postulated for the Water Pipit (*Anthus spinoletta*) (Verbeek 1970), the Golden-cheeked Warbler (*Dendroica chrysoparia*) (Pulich 1976), and the Ovenbird (Hahn 1937).

Eleven of 14 species in the sample of wanderers (Table 2) are single-brooded, long-distance migrants. We suggest that these birds abandon their breeding territories shortly after completion of breeding and wander in search of abundant food resources that are available in many natural, terrestrial habitats of the southeast during the summer and early fall months. The species that did not disappear from our site were either permanent residents (Tufted Titmouse, Carolina Wren, Northern Carolina) or double-brooded migrants (Gray Catbird, White-eyed Vireo, Common Yellowthroat).

Postbreeding, premigration wanderering is supported by the fact that the birds neither sang nor gave call notes. These same species sing and call vigorously in defense of breeding territories, and they average 1–2 min/h in defense of winter feeding territories (Rappole and Warner 1980). Even many transients defend feeding territories, using call notes and displays (Rappole and Warner 1976). The silence of these birds at our study site in July and August, 1980, their lack of site tenacity, and their lax preferences with regard to habitat selection all indicate that food was not limiting, and that intra- and interspecific competition for resources were not particularly stringent during this postbreeding period.

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Spring migration of Long-eared Owls and Northern Saw-whet Owls at Nine Mile Point, New York.—Although Long-eared Owls (*Asio otus*) and Northern Saw-whet Owls (*Aegolius acadicus*) occur in New York State throughout the year, they are observed in greatest numbers during migration and in winter. Although hawk migration in spring has been studied for years along the southern shore of Lake Ontario (Haugh and Cade 1966, Smith and Muir 1978, Moon and Moon 1985), there are no published studies of owl migration there. Here we summarize data collected along the south shore of Lake Ontario on the spring migration of Long-eared Owls and Northern Saw-whet Owls during the springs of 1981 through 1986.

Study area and methods.—The study was conducted on the Richard A. Noyes Wildlife Sanctuary at Nine Mile Point, New Haven, Oswego County, New York, along the southeastern shore of Lake Ontario (Fig. 1). The 90-acre sanctuary is composed of northern hardwood forest (*Acer rubrum, Quercus rubra, Fagus grandifolia, Tsuga canadensis*), red pine (*Pinus resinosa*) plantations, and shrub (*Viburnum dentatum, Cornus* spp., *Alnus rugosa*) habitat.

Mist nets (30–114 mm mesh, 5–12 m length) were placed within wooded and shrub areas, across trails, and along ecotones on a total of 117 nights (9, 16, 18, 37, 18, 19; 1981–1986, respectively). The banding station was in operation from early March (weather permitting) until late April or mid-May, when migration appeared to end. The number of nets operated on a given night ranged from 4 to 40, depending upon weather conditions and the number of assistants available. The total effort for all years was 25,023 net-h. Nets were open from before sunset to after sunrise, unless weather conditions forced the closure of all or some of them. Nets were checked at 1 to 2.5 h intervals, depending upon weather conditions. For each owl captured, the date and time (EST), age and sex, location of the capture, and weather

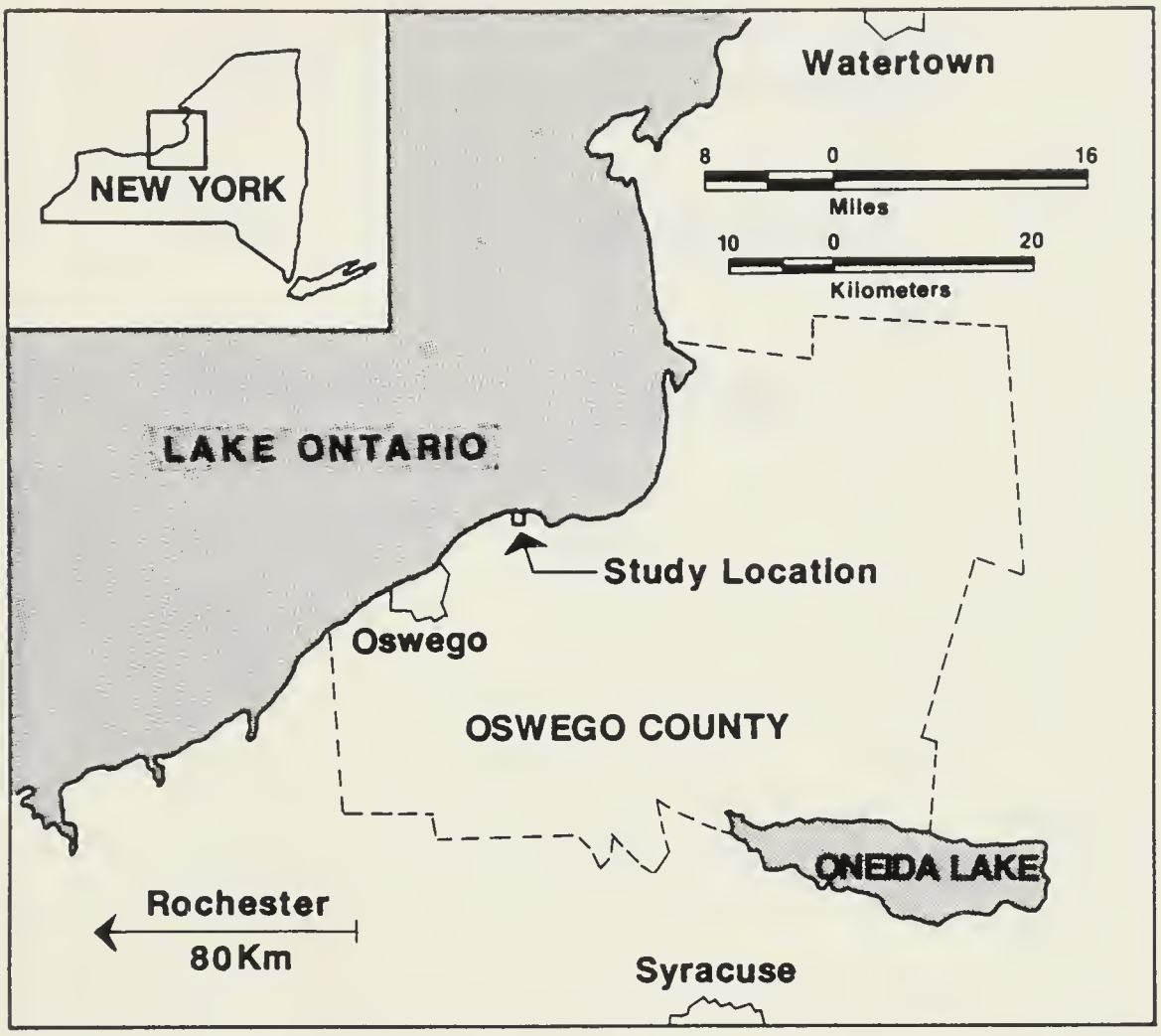

FIG. 1. Location of study area.

conditions at that time were recorded. Owls were aged (remige molt and fault bar pattern) and sexed (wing chord) based upon the criteria set forth in the Banding Manual (U.S.F.W.S. 1977).

Migration dates.—A total of 139 owls (37 Long-eared, 102 Northern Saw-whet) was captured. From 0 to 13 Long-eared Owls were captured each year, along with from 4 to 33 Northern Saw-whet Owls (Table 1). The initiation of Northern Saw-whet Owl migration apparently shifts from year to year, depending upon spring weather conditions. For example, in 1982, the first saw-whet was captured on 13 March and the last on 16 April; there was a peak between 24 March and 30 March, when 9 out of the 15 birds banded during the year were captured. This contrasts with 1984 when winter weather conditions persisted into the first week of April; all 27 birds for that year were captured after 28 March, with a peak of 9 being captured between 12 and 14 April. In 1983, recurring periods of unfavorable weather prolonged the saw-whet migration, which was relatively steady from 17 March to 4 May. In general, Northern Saw-whet Owl migration occurred between 16 March and 4 May. The earliest saw-whet captured (5 March 1983), which was recaptured at the site 7 days later, was probably a winter resident. Long-eared Owl migration, which occurred between 21 March and 14 April, did not appear to be as weather-dependent. Thirty-three of the 37 individuals were captured during this time period. Three individuals captured after 24 April probably were local breeding birds.

TABLE 1

SUMMARY OF OWL CAPTURES BY 5-DAY INTERVALS

	Northern Saw-whet Owls							Long-eared Owls						
Date interval	1981	1982	1983	1984	1985	1986	Total	1981	1982	1983	1984	1985	1986	Total
1–5 March	–[a]	–	1	–	–	–	1	–	–	0	–	–	–	0
6–10 March	–	–	0	–	1	–	1	–	–	0	–	0	–	0
11–15 March	–	1	0	0	0	1	2	–	0	0	0	0	0	0
16–20 March	–	0	7	0	1	0	8	–	0	0	0	0	0	0
21–25 March	–	5	0	0	0	4	9	–	2	0	1	0	1	4
26–30 March	1	5	2	2	1	10	21	0	2	0	0	1	3	6
31 March–4 April	1	0	4	2	0	2	9	0	0	1	4	0	4	9
5–9 April	0	0	2	2	1	0	5	0	0	2	4	3	0	9
10–14 April	0	2	1	9	1	0	13	0	0	0	3	2	0	5
15–19 April	1	2	0	2	0	0	5	0	0	0	0	1	0	1
20–24 April	0	0	2	3	0	1	6	0	0	0	0	0	0	0
25–29 April	1	0	6	5	0	0	12	0	0	0	1	0	0	1
30 April–4 May	0	–	7	0	0	–	7	0	–	2	0	0	–	2
5–9 May	–	–	1	0	–	–	1	–	–	0	0	–	–	0
10–14 May	–	–	0	1	–	–	1	–	–	0	0	–	–	0
15–19 May	–	–	–	1	–	–	1	–	–	–	0	–	–	0
20–24 May	–	–	–	0	–	–	0	–	–	–	0	–	–	0
Annual totals	4	15	33	27	5	18	102	0	4	5	13	7	8	37

[a] No nets set.

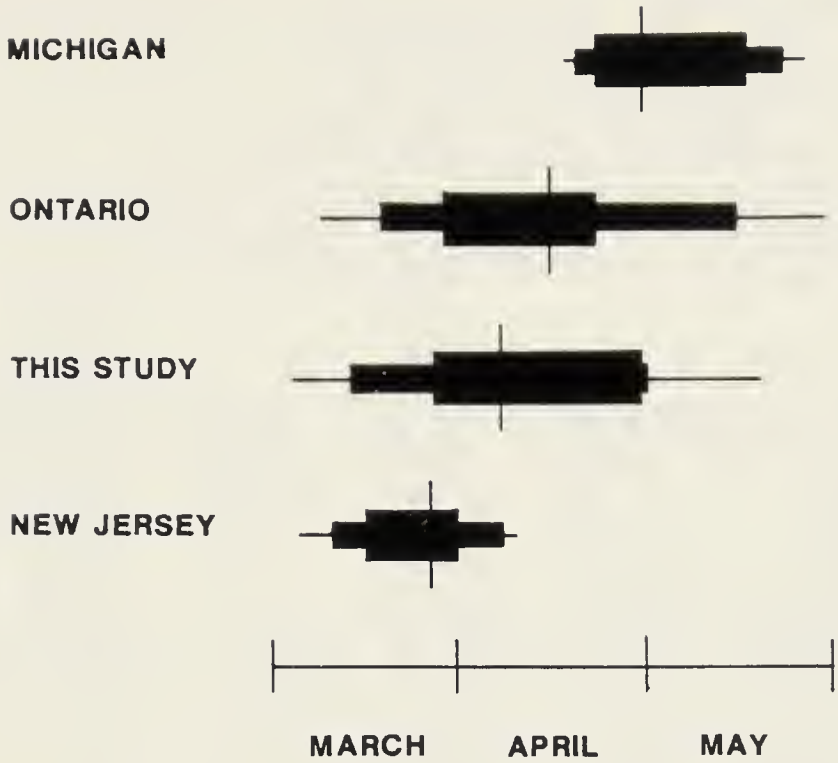

FIG. 2. Timing of spring migration of Northern Saw-whet Owls. Vertical bars indicate mean date, wide bars indicate 66% of the bandings, medium bars, 90%, and narrow lines the range. Data for Michigan, Ontario, and New Jersey are taken from Holroyd and Woods (1975).

Bull (1974) gives no dates on the spring migration of Long-eared Owls. For Northern Saw-whet Owls, he lists only one record, 10 birds observed along the Lake Ontario shoreline on 3 April 1952. In the Niagara Frontier (western New York), Beardslee and Mitchell (1965) reported the spring migration of Long-eared Owls as occurring from 29 March to 26 April, with saw-whets migrating from 21 March to 9 May. Our data are similar to those described by Holroyd and Woods (1975) who used banding data collected between 1955 and 1969 to analyze the migration of the Saw-whet Owl in eastern North America (Fig. 2).

Nocturnal activity pattern.—Our data (Fig. 3) indicate that Northern Saw-whet Owls migrate later in the evening than do Long-eared Owls. Long-eared Owls are known to leave their diurnal roosts approximately 30 to 60 min after sunset (Glass and Neilsen 1977, Bosakowski 1984). In their fall studies of saw-whets, Weir et al. (1980) had proportionately fewer captures of this species in the time period around sunset. For both species, many of the birds that were captured near sunrise were probably individuals that were searching for roost sites or hunting just prior to roosting.

Age analysis.—All but one Long-eared owl was aged as AHY (after hatching year). Therefore, no determination concerning the timing of migration in relation to age class of Long-eared Owls can be made. Northern Saw-whet Owls were assigned to three age categories: 31 ASY (after second year), 9 SY (second year), and 62 AHY. Based upon the date of first capture in each year, SY birds arrived on the average 11 days later than did ASY birds. Because of the large proportion of AHY birds, however, these data are inconclusive.

Wind direction.—Fifty-nine percent of the Northern Saw-whet Owls were captured on winds with a southerly component ($\chi^2 = 18.47$, $P < 0.01$). Fifty-two percent of the Long-eared Owls were captured on southeasterly to westerly winds. Twenty-four percent of the

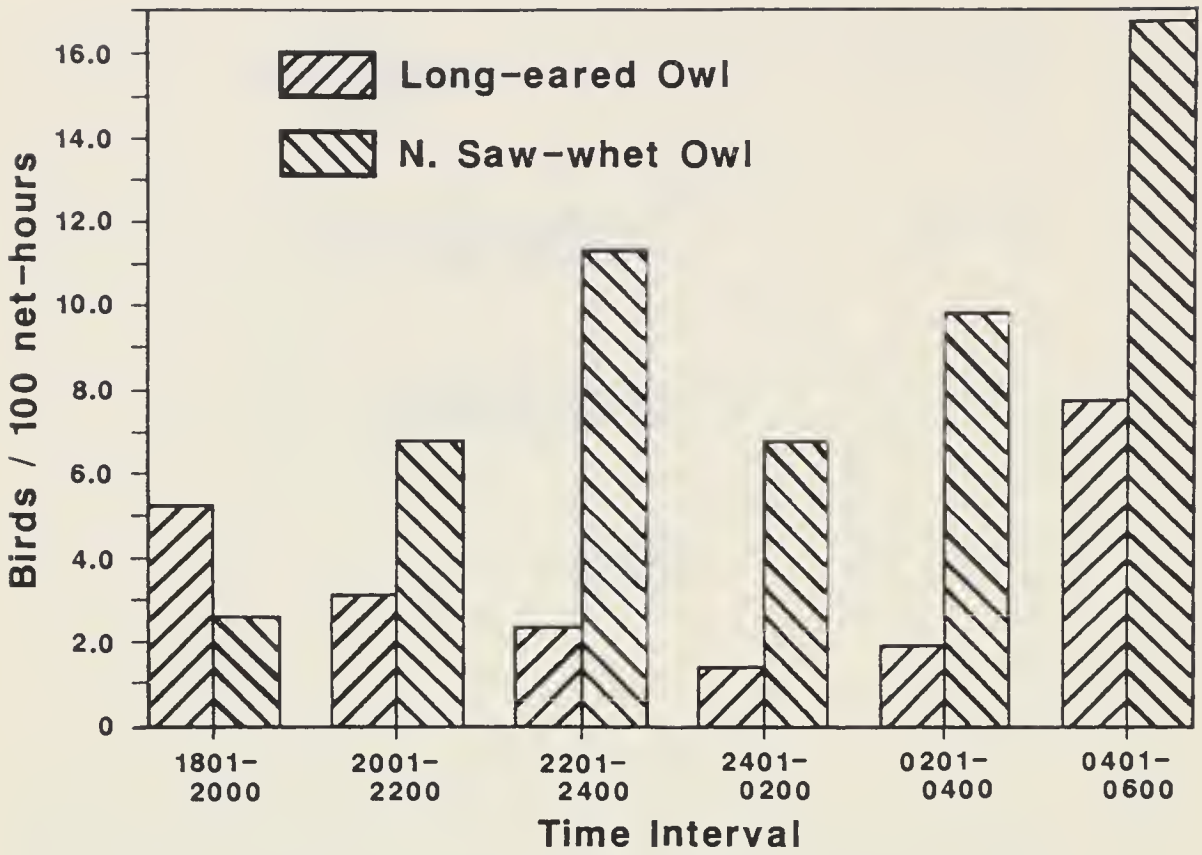

FIG. 3. Owl captures per 100 net-h within nightly time intervals.

Northern Saw-whet Owls and 32 percent of the Long-eared Owls were captured when winds were calm at the site. Thus, both species avoided migrating on northwesterly to easterly winds.

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Nest-box use by Prothonotary Warblers (*Protonotaria citrea*) in riverine habitat.—Nest boxes are often used in studies of cavity-nesting species (e.g., Dahlsten and Copper 1979), and they have been particularly important in conservation studies of Eastern Bluebirds (*Sialia sialis*) (Zeleny 1976). Many cavity-nesting birds have been shown to prefer nest boxes to natural cavities (McComb and Noble 1981, Brawn 1984).

The Prothonotary Warbler (*Protonotaria citrea*) is one of only two cavity-nesting wood warblers in North America. They nest in swampy or flooded forest areas (Bent 1953), and their populations may be declining due to loss of habitat (Graber et al. 1983). Although nest box use has been well documented for many secondary cavity nesters, little work of this kind has been conducted on the Prothonotary Warbler.

In 1984, we conducted an evaluation of the effects of industrial fluoride contamination on the egg viability and clutch size of Prothonotary Warblers. We erected nest boxes to facilitate finding nests in our study areas. Here, we report on the use of three different types of nest boxes by Prothonotary Warblers, along with factors that may influence their selection.

Study area and methods.—In March 1984 we placed 301 nest boxes in flooded riparian habitat along the Tennessee River in Benton and Humphrey counties, Tennessee. Woody vegetation in the river floodplain is dominated by willows (*Salix* spp.), buttonbush (*Cephalanthus occidentalis*), sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), elms (*Ulmus* spp.), and hackberry (*Celtis occidentalis*).

We erected 145 cardboard milk cartons (Fleming and Petit 1986), 84 standard wooden bluebird boxes (Zeleny 1977), and 72 tubes of black PVC pipe (30-cm long × 10.2-cm diameter) with plastic caps attached on top and bottom. The volume of each box was measured from the bottom of the box to the lower lip of the entrance hole. Tubes had the greatest volume (1226 cm^3), followed by wooden boxes (1218 cm^3) and milk cartons (903 cm^3), respectively.

All boxes had entrance holes approximately 3.75 cm in diameter, centered 5 cm from the top of the box. Milk cartons and tubes were spray-painted gray in order to make them less conspicuous. Wooden boxes were not painted because their natural wood color made them sufficiently inconspicuous. All boxes were placed on trees, 1.5–2.0 m above the water surface

TABLE 1

PROTHONOTARY WARBLER USE OF THREE TYPES OF NEST BOXES IN RIPARIAN HABITAT ALONG THE TENNESSEE RIVER IN WEST CENTRAL TENNESSEE, 1984

Nest site	Sites available[a]		Sites used[b]	
	No.	%	No.	%
Milk carton	143	48.2	79	67.5
PVC tube	71	23.9	32	27.4
Wooden box	83	27.9	6	5.1
Total	297	100.0	117	100.0

[a] Nest boxes containing species other than Prothonotary Warblers are not included.
[b] G-test of next box use vs availability: $G = 60.78$, df = 2, $P < 0.001$.

(most nests in natural cavities were within this range), and were erected before Prothonotary Warblers arrived in the spring.

We placed boxes at about 40-m intervals along the main shoreline and on the periphery of islands in the river. All three box types were distributed haphazardly in each stretch of suitable habitat.

Boxes were checked for active nests at least bi-weekly from 15 May–1 August 1984. Log-likelihood ratio (G) tests for contingency analysis were used to test for nonrandom patterns of box occupancy.

Prothonotary Warbler clutches initiated (first egg laid) before 25 June were considered to be first clutches (early), and those initiated after that date were considered to be second clutches (late). Clutch sizes were compared among nest box types in early and late nests using two-way analysis of variance (ANOVA).

We also noted frequencies of parasitism by Brown-headed Cowbirds (*Molothrus ater*) and predation in the different box types. Nests were assumed to have been depredated if young or eggs disappeared before the predicted fledging date, or if the nest was destroyed. The rate of predation we report here may be slightly low because not all nests were monitored from egg-laying through fledging. Most, however, were followed at least through incubation.

Results.—Prothonotary Warblers nested in 117 (38.9%) of 301 nest boxes, Tree Swallows (*Tachycineta bicolor*) used three boxes, and a pair of Tufted Titmice (*Parus bicolor*) used one. Boxes with the titmice and swallows were omitted from the analysis because they were unavailable to the warblers.

Prothonotary Warblers showed a significant preference for milk cartons and an avoidance of wooden boxes (Table 1). Tubes were used in approximate proportion to their availability.

Percentages of boxes used did not differ between early and late clutches among the three nest-box types. Thirteen (11.0%) of the 117 nest boxes used by Prothonotary Warblers were used twice during the breeding season. Renesting attempts occurred in similar proportions in cartons (9.9%) and tubes (15.2%); the warblers apparently did not renest in wooden boxes.

Clutch size did not differ significantly among nests in different nest box types ($F = 0.31$, df = 2, $P > 0.05$). Although early clutches were significantly smaller than late clutches ($F = 9.10$, df = 1, $P < 0.01$), this trend was independent of the type of box ($F = 0.09$, df = 1, $P > 0.05$).

Cowbird parasitism occurred in 23.0% of warbler nests. Cartons, tubes, and wooden boxes had parasitism in 20 of 79 (25.3%), 6 of 32 (18.8%), and 1 of 6 (16.7%) boxes, respectively (no significant differences in parasitism rates; $G = 0.72$, df = 2, $P > 0.05$). Only 3 (2.6%) of the 117 nests were depredated.

Discussion.—We suggest several reasons why Prothonotary Warblers more readily nested in milk cartons and tubes than in wooden boxes. One obvious difference between the box designs was volume. Peterson and Gauthier (1985) showed that cavity volume was the single most important factor influencing nest-site selection by five species of cavity-nesting birds in Canada. Greater volume of a nest box may discourage use by Prothonotary Warblers because of increased effort involved in filling the box (nearly to the entrance hole) with nesting material (pers. obs.).

Although we attempted to place the three box types randomly throughout the habitat, the design of the wooden boxes limited their placement to larger trees (diameter at nest box height >15 cm). Cartons were affixed with strapping tape to trees, allowing them to be placed on trees of smaller diameter. Tubes were also fastened to smaller trees. For nests in natural cavities on our site, mean diameter at cavity height was 13.6 cm (N = 11). Thus, our data may be biased by substrate size.

As wooden boxes were left unpainted while cartons and tubes were painted gray, wooden boxes may have been less conspicuous to the birds. However, wooden boxes were the bulkiest of the three box types, and enough were present in the study area that it seems unlikely that the birds overlooked them.

Incidence of predation was very low, and rates of brood parasitism were similar in the different box designs, suggesting that the suitability of a nest box was not based on its susceptibility to either of these factors. Although we do not have data to show reproductive success (e.g., number of young fledged), Prothonotary Warbler clutch sizes were not statistically different in cartons and tubes.

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Sage Grouse use of snow burrows in northeastern Nevada.—Apparently all species of *Tetraoninae* roost in snow for thermal conservation, provided that the snow is sufficiently deep and no ice crust occurs at the surface (Kuzmina 1961). However, the type of roost may vary with snow conditions or weather. We distinguish between 2 roost types: "snow forms" and "snow burrows." Snow forms are shallow depressions or open bowls in the snow in which the dorsal surface of the bird is exposed. Snow burrows are deep holes or tunnels in which the bird actively burrows completely under the snow surface. The difference in the thermal protection afforded by each roost type may be quite large. Gullion (1970) found that temperatures under 20 cm of soft snow in hardwood stands were between −3° and −12°C when ambient air temperature was as low as −35°C. Snow burrows provide a warmer microenvironment than do snow forms, and the covering of snow reduces radiant heat loss. Because of differences in thermal protection provided by snow forms and snow burrows, we recommend that ambiguous terms such as dug outs, snow roosts, or roost depressions be avoided when describing roost sites or behavior.

The use of snow burrows has been reported for Ruffed Grouse (*Bonasa umbellus*) (Bump et al. 1947), Sharp-tailed Grouse (*Tympanuchus phasianellus*), Greater Prairie Chicken (*T. cupido*) (Ammann 1957), Willow Ptarmigan (*Lagopus lagopus*) (Irving 1960), White-tailed Ptarmigan (*L. leucurus*) (Braun and Schmidt 1971), Capercaillie (*Tetrao urogallus*), Black Grouse (*Lyrurus tetrix*), and Hazel Grouse (*Testrastes bonasia*) (Formozov 1946). Although Sage Grouse (*Centrocercus urophasianus*) are exposed to subfreezing temperatures and snow conditions that are often suitable for snow burrowing, we could find no published reports of snow burrowing by this species. Griner (1939:42), Ihli et al. (1973:75), and Beck (1977: 23) reported Sage Grouse roosting in "holes," "snow caves," and "roost depressions," respectively. Their descriptions suggest that snow forms, rather than snow burrows, were observed. Patterson (1952:179) reported Sage Grouse used snow forms but found no evidence that they burrowed.

We observed 83 snow burrows at 13 different locations while conducting a Sage Grouse winter movement study in northeastern Nevada from 1982 to 1985. On all but one occasion, burrowing occurred within one week of snowfall. Minimum temperatures during the periods of snow-burrow use were < -10°C in all but one instance.

Snow burrows occurred in unpacked, soft drifts on the lee side of shrubs (N = 21) and in open, level areas with no shrub cover visible above the snow (N = 62). "Drift burrows" were made by birds tunneling into the drift on one side and exiting from the other. Entrance holes were plugged by the snow roof collapsing behind the birds. Mean length of drift burrows was 56 cm (range = 48–63 cm, N = 21). Mean depth (from snow surface to bottom of the burrow) was 30 cm (range = 26–35 cm, N = 21). The mean "roof" thickness above the roost site (i.e., above the dropping accumulation) was 9 cm (range = 8–11, N = 14). "Open-snow burrows" were made in soft, dry snow >25 cm deep and had a mean length of 110 cm (range = 74–152 cm, N = 30) and mean depth of 35 cm (range = 25–39 cm, N = 30). The mean roof thickness was 13 cm (range = 10–16 cm, N = 13). Open-snow burrows were longer (t-test, df = 49, $P < 0.001$), deeper (df = 49, $P < 0.001$), and had more snow over

the burrow (df = 25, $P < 0.001$) than did drift burrows. These differences may have been due in part to the width and depth of snow drifts, which effectively limited the length or depth of a burrow. (Photos of a drift burrow [V06-1-014] and an open-snow burrow [V06-1-015] have been deposited at VIREO.)

The type of burrow observed varied with snow conditions. Drift burrows were used when drifts provided the only deep snow in which to burrow. Open-snow burrows only were observed when soft, dry snow >25 cm was available. Winter (15 November–15 March) weather data for 1983–84 and 1984–85 indicated that in over 75% of the precipitation events, the daily minimum temperature was at least 10°C lower for several days following precipitation. Therefore, dry snow was available for several days after most snow storms.

The widespread occurrence of snow burrowing among tetraonids suggests that the behavior is adaptive (i.e., it affects either survival *or* reproductive performance). Use of snow burrows has been suggested as a factor in survival of Ruffed Grouse (Gullion 1970) and White-tailed Ptarmigan (Braun and Schmidt 1971), and increased losses of Hazel Grouse and Black Grouse have occurred when snow cover was lacking and temperatures were extreme (Kuzmina 1961). But conclusive evidence that snow burrowing increases survival of Sage Grouse or other grouse species has not been reported.

For Sage Grouse, the timing and pattern of weight changes suggest that this behavior is linked to reproductive performance. Sage Grouse gain weight during winter, with most of the increase occurring between January and March, and peak weights occurring just prior to the beginning of breeding activities (Beck and Braun 1978). Male Sage Grouse lose weight during the strutting period, and losses for females are probably associated with incubation. Therefore, late winter weight gain appears related more to energy demands of breeding than to overwinter survival. If this is true, a behavior that conserves energy, such as snow burrowing, would contribute to breeding condition.

For an activity to contribute to energy saving, it must help maintain the body temperature above the temperature below which a resting grouse must increase its metabolic rate to meet environmental demands for heat. This lower critical temperature (LCT) is unknown for Sage Grouse; therefore, the actual contribution of snow burrowing to energy conservation cannot be determined. The LCT for captive Ruffed Grouse, however, ranged from a mean of −6°C in February to 0.3°C in March (Rasmussen and Brander 1973). The birds on our study area were exposed to temperatures below −10°C for 81 and 92 nights between 15 November and 15 March of 1983–84 and 1984–85, respectively. Thus, snow burrowing probably was an effective energy conservation behavior for more than 50% of the winter nights.

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Size of host egg and egg size in Brown-headed Cowbirds.—The North American Brown-headed Cowbird (*Molothrus ater*) is a brood parasite that lays its eggs in a variety of other birds' nests. Cowbirds exhibit variation in egg size both within and among females (Ankney and Johnson 1985), but it is unknown if this variation follows predictable intraclutch patterns as it does in some icterines (Howe 1976, Weatherhead 1985). Several studies on a variety of species have shown that the probability of survival of a particular hatchling increases with egg size or hatchling weight (e.g., Parsons 1970, O'Connor 1979). Here I report the results of a study aimed at determining whether cowbird egg size varies as a function of host egg size.

I measured cowbird eggs in 143 clutches parasitized with one or two (total 168) cowbird eggs in the collections of the Royal Ontario Museum, the National Museum of Canada, and Cornell University. Nests with more that two cowbird eggs were not used as they were assumed to be dump nests (Harrison 1975). Egg sets came from Ontario and Quebec (78%), the northeastern United States (13%), and the Canadian prairie provinces (9%). Although the last group probably included individuals of the race *artemisiae*, they showed no difference in mean size from those of the nominate race. The egg sets were from 42 species of seven families.

I measured length (L) and breadth (B) of each egg to the nearest 0.05 mm and used κLB^2 as an estimator of egg volume, where κ is a constant derived from empirical studies. For cowbirds ($\kappa = 0.515$; Nolan and Thompson 1978), the largest egg was 1.63 times greater than the smallest. For host eggs ($\kappa = 0.524$; Romanoff and Romanoff 1949:108), the largest egg was 4.78 times greater than the smallest.

There was no indication of a correlation between the estimated volumes of cowbird and host eggs ($P > 0.01$), nor was there a correlation between cowbird egg volume and host weight ($P > 0.01$). I also estimated the volumes of host nests using dimensions given in Harrison (1975); I used $\frac{1}{2}(4/3)\pi r^3$ (where r = [depth + diameter]/3) as an estimator of nest volume. There was no relationship between cowbird egg size and host nest volume ($P < 0.01$) for the 32 host species for which estimates were possible (142 eggs).

Variation in egg size may be imperfectly predictable to the laying cowbird, and other factors such as environmental conditions (Ankney and Johnson 1985), nutritional state and clutch size (Howe 1976), and age (Blank and Nolan 1983) may also affect the size of eggs laid. Furthermore, the utility of egg size variation predictability may be secondary to the availability of hosts for any one laying event.

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Polygyny and double-brooding in the Least Flycatcher.—Polygyny is considered rare among the flycatchers (Skutch 1960), and has been detected in only four species in North America (Ford 1983, Prescott 1986). Two cases of bigamy in the Acadian Flycatcher (*Empidonax virescens*) and one case in the Willow Flycatcher (*E. traillii*) are the only instances recorded in the genus (Mumford 1964, Prescott 1986). Here we report on a polygynous mating and two cases of double-brooding in the Least Flycatcher (*E. minimus*).

Study area and methods.—We studied Least Flycatchers nesting in the forested dune ridge along the south shore of Lake Manitoba, Manitoba (see MacKenzie 1982 for description of study area). All observations were made in 1985 when flycatchers nested at a density of 4.9 pairs/ha, with approximately 79 pairs on the study area (Briskie 1985). The polygynous male and both the primary and secondary females were individually marked with color bands or paint. We did not know the order in which the pairbonds were formed, so we assumed the first female to initiate laying was the primary female. The second double-brooding attempt involved an unbanded male and a banded female.

Growth and parental feeding were examined in all three nests of the polygynous male. Nestlings were weighed on an Ohaus scale to the nearest 0.1 g at 10 days of age. At 8 days nestlings were banded with aluminum and year-specific color bands. Feeding observations were made from 15 to 20 m with a 20× spotting scope. Numbers of prey delivered by each sex within a 2-h period were recorded. Observations were made when nestlings in the primary nest were 8 and 11 days old. Observations at the secondary nest were made only when the young were 11 days old. The second nest of the primary female was observed at the ages of 2 and 11 days.

Nesting chronologies.—The nest of the primary female was found on 2 June. The first of four eggs appeared on 6 June. Hatching began early in the evening of 21 June and was completed by the morning of 23 June. The second egg laid was damaged and did not hatch. It was found beneath the nest on 25 June and contained a 10–12-day-old embryo. The first nestling fledged on 6 July; the two remaining young fledged the next day.

The nest of the secondary female was found 21.5 m from the nest of the primary female on 7 June. The first egg was laid on 9 June, 3 days later than the first nest. The clutch of four was completed on 13 June. Hatching began in the late afternoon of 24 June, and all four nestlings were present by the morning of 26 June. Three nestlings fledged on 9 July; the last left the next day.

On 14 July, the second nest of the primary female was found 3.5 m from her first nest. The first of three eggs was laid on 15 July, eight days after the first brood fledged. One nestling died during hatching; however, the two remaining nestlings fledged on 16 August. The male and female remained mated for both broods.

The second case of double-brooding was initiated on 22 July. The first brood of this female was initiated on 12 June. Both nests were built in the same tree crotch. Four eggs were laid in each clutch, but only three young fledged from the first brood (one nestling was removed for use in brood manipulation experiments [Briskie 1985]). Seven days elapsed between the fledging of the first brood and the laying of the first egg of the second brood. The second nest was preyed upon on 6 August, the day the clutch was due to hatch.

Parental feeding and growth.—The polygynous male fed nestlings in both first broods, but most of the prey items were delivered to the young of the secondary female. During 2 h of observation, 55.1% of the 69 prey items fed to young in the secondary nest were delivered by the polygynous male. In contrast, the polygynous male delivered only 8.9% of the 112 items brought to young in the primary nest during 4 h of observation. Deliveries of prey items by the male to the second brood of the primary female (44.7% of 38 prey

items during 4 h of observation) equalled those of the female; however, the male did not feed the young after they fledged.

Despite the low investment in feeding by the male, nestlings in the primary nest grew as well as did nestlings in both the secondary nest and the second nest of the primary female (mean mass at 10 days of primary brood: 10.6 g, N = 3; secondary brood: 8.9 g, N = 4; second brood of primary female: 9.6 g, N = 2).

Discussion.—To our knowledge this is the first report of polygyny in the Least Flycatcher. Although we found over 125 flycatcher nesting attempts on our study area in 1985, only a few of the birds were color marked. As a result, we do not know what percent of the population was polygynous.

Double-brooding in Least Flycatchers has been reported previously by Hoffman (1901), Bent (1942), and Walkinshaw (1966), although none of these researchers mentions whether the birds they studied were individually marked. Using marked birds, we observed double-brooding in a minimum of 2 of 79 pairs (2.5%) on the study area in 1985. Young fledged successfully in only one of the nests.

Least Flycatchers arrive on our study area in mid-May and depart for the wintering areas in Central America by mid-July (Sealy and Biermann 1983). Typically, this allows only one successful nesting attempt per season. In order to raise a second brood, pairs must remain approximately 40 days longer than single-brooded birds (pers. obs.). Double-broods were the last clutches to be initiated and the last broods to fledge in 1985. By remaining on the breeding grounds adults and young possibly face unfavorable weather and lower insect abundance. As adult Least Flycatchers are territorial on the wintering grounds (Rappole and Warner 1980), delaying migration may also prevent birds from establishing and maintaining territories in Central America (Sealy and Biermann 1983). Together, these factors may have selected against a high frequency of double-brooding at this latitude.

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Short-billed Dowitchers associate closely with Lesser Golden-Plovers.—On their European breeding grounds Dunlins (*Calidris alpina*) often feed in intimate association with Greater Golden-Plovers (*Pluvialis apricaria*), even when the latter are dispersed on their breeding territories. Dunlins appear to associate with the plovers for vigilance, and typically one (but sometimes 2–3) Dunlin follows an individual plover (Byrkjedal and Kålås 1983, Ornis Fennica 60:10–15; Thompson and Thompson 1985, Ibis 127:559–562).

While studying behavior of breeding Lesser Golden-Plovers (*P. dominica*) at Churchill, Manitoba, in 1986, I observed 5 cases of Short-billed Dowitchers (*Limnodromus griseus*) associating with Lesser Golden-Plovers on the tundra in a manner closely resembling the Dunlin–Greater Golden-Plover association. (1) On 26 June, I entered a golden-plover territory and found the female feeding in a patch of sedge tundra together with a Short-billed Dowitcher. The dowitcher followed the golden-plover at distances of from 0.5 to 1.5 m, while constantly feeding. I deliberately flushed the birds three times, and each time the dowitcher stayed within 1.5 m of the golden-plover, resuming feeding once they had alighted. I left the territory after about 35 min, and the birds were still together. (2) At a scheduled observation on 7 July at another golden-plover territory, the male flew up and landed on a piece of sedge tundra with a dowitcher following closely. Both birds started to feed at once, and the dowitcher followed the golden-plover at distances of from 0.5 to 1 m. During the 6 min that they stayed in view, the golden-plover attacked the dowitcher twice by rushing towards it with lowered head, but did not succeed in driving the dowitcher away. (3) At a nest inspection in the evening of 7 July the same golden-plover male (color marked) was accompanied by a dowitcher as soon as the plover left the nest. The male stood vocalizing (giving a two-syllable alarm call) about 20–30 m off, when the dowitcher flew up to him from a patch of sedge tundra about 60 m away. The dowitcher started to feed within 0.5 m of the plover. I observed the birds together for about 10 min. When I retreated, the golden-plover approached the dowitcher (as in case 2), which subsequently stood and watched as the golden-plover walked back to the nest. (4 and 5) On 13 July I saw a dowitcher feeding together with a female golden-plover in one territory and another one feeding along with a plover of unknown sex in a patch of sedge tundra near a second territory. In both cases the dowitchers followed the movements of the golden-plovers within 1 m distance during the 2–3 min it took me to pass by.

As do Dunlins in association with Greater Golden-Plovers, the dowitchers (1) walked closely behind the golden-plovers, following their movements on the ground, (2) took flight

and alighted with the golden-plovers, and (3) fed intensely when with the plovers. The plovers tried to chase their company without success, as is the case with Greater Golden-Plovers and Dunlins (Byrkjedal and Kålås 1983).

Except when several shorebird species flocked on common feeding grounds (e.g., along the shore and at muskeg ponds), I never saw dowitchers associate with any of the other species on the tundra, although both Hudsonian Godwits (*Limosa haemastica*) and Whimbrels (*Numenius phaeopus*) were numerous. Plovers may be attractive "watch dogs" for other birds, because they feed in run-stop-peck sequences, which may provide them with a better opportunity for detecting predators when feeding than exists in shorebirds that feed by probing. The large plovers may be especially attractive as partners because their height gives them a better view than small plovers have, and their size makes them more easily seen by predators (e.g., hawks), so that they may have to be more vigilant than the smaller plovers. I suggest that dowitchers associated with golden-plovers for vigilance, but data on flushing distances and feeding activities of dowitchers in association with golden-plovers and with conspecifics are needed.

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Foraging behavior and diet of Lesser Sandhill Cranes in low arctic tundra near Eskimo Point, Northwest Territories, Canada.—Although the Lesser Sandhill Crane (*Grus canadensis canadensis*) is commonly observed in the south during migration and in winter, relatively few observations have been made of the behavior and foraging strategies of this subspecies during the breeding season in the arctic. Surveys done in the United States during the nonbreeding season indicate Sandhill Cranes forage on a wide variety of food items, including insects, grubs, spiders, rootlets, herbage, grain, berries, and occasionally mice and young birds (Bent 1926, Walkinshaw 1949, Salt and Wilk 1958, Littlefield 1976). Harvey et al. (1968) observed cranes on the breeding grounds at McConnell River, N.W.T., where they fed on Snow Goose (*Chen caerulescens*) eggs, Willow Ptarmigan (*Lagopus lagopus*) young, and varying lemmings (*Dicrostonyx groenlandicus*).

During May, July, and August 1985 I observed Lesser Sandhill Cranes at close range at Eskimo Point, Northwest Territories, Canada (61°06′N, 93°59′W). The first cranes were seen 18 May 1985, and their numbers increased dramatically with each passing day. At this time of year, snow covered the ground (ca 25 cm) except on the tops of the higher eskers, which were mostly covered with a thin carpet of lichens (ca 77%), comprised mainly of *Coelocaulon divergens, Cetraria nivalis,* and *Cetraria cucullata* (Mallory and Heffernan, in press). Lakes and rivers were still frozen, except in small areas where the water was shallow and the currents strong. The first birds occurred in tight flocks of 6 to 12 individuals that fed on lichens in the snow-free areas. Cranes were never observed fishing in or along the openings in the rivers or lakes, but they did scavenge at sites where fish remains were left by local fishermen. Birds remained in small flocks through the end of May, and I saw no evidence that pairs separated from the main flocks to establish territories. As snow melted, feeding occurred farther down the eskers. During this time, cranes appeared to subsist on a diet composed mainly of lichens and old growth vegetation. Data (Krapu et al. 1985) on

fat deposition occurring on spring staging areas indicate that cranes increase their fat reserves during the northern migration from an average of 250 to 990 g/bird. These reserves would presumably allow individuals to survive on the breeding grounds earlier in the season when food is scarce.

In July, a blind was built on the top of an esker, approximately 50 m from an arctic fox (*Alopex lagopus*) den that contained a mated pair and 11 pups. Prey brought back to the den site was mainly young Snow Geese and a few arctic ground squirrels (*Spermophilus parryii*). Small pieces of food were often left near the burrow entrances. On 7 occasions, when the foxes were below ground, pairs of adult cranes with young approached the den site and put their heads 30 to 60 cm into the burrows. The smaller young cranes often entered the burrows completely. Small pieces of meat (mainly young Snow Geese) were given to or placed in front of the young cranes by the adults. Sibling rivalry was observed among the young for these food items, and the larger offspring frequently chased the smaller chick away from the area being searched. These excursions lasted for approximately 20 min, after which the cranes returned to the wet meadow areas. This behavior was not observed in May, before food was available at the site, nor in August when the fox pups were active outside the den.

On one occasion, a pair of cranes with a single young was observed foraging in a wet meadow area. The adults walked slowly to each hummock, and with heads lowered, inspected the base, often cocking their heads. After approximately 5 min, one of the adults made a quick stab with its bill and stood up holding a varying lemming. The adult ran ahead a short distance followed closely by the young, which begged and was fed the entire carcass. Trapping data indicated that small mammal populations were high during 1985.

In August, cranes foraged on the upper slopes and tops of the eskers. During this period, the mast of the season was ripening, and cranes consumed large numbers of berries, especially crow berry (*Empetrum nigrum*), bilberry (*Vaccinium uliginosum*), and mountain cranberry (*Vaccinium Vitis-idaea*).

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Suspected adult intraspecific killing by House Wrens.—Although infanticide has been observed in several species of birds (Mock 1984), the killing of adult conspecifics is far less common (Lombardo 1986). The purpose of this note is to report the possibility of the intraspecific killing of adult House Wrens (*Troglodytes aedon*).

In 1984 we initiated a study of House Wren reproductive strategies at Presqu'ile Provincial Park in southern Ontario (see Belles-Isles and Picman 1986a for a description of our methods and study area). In 1984, 1985, and 1986; 60, 92, and 69 wren nest boxes (entrance diameter = 3 cm), respectively, were distributed throughout the study area. In all 3 years, most boxes were occupied by House Wrens. In May of 1986, we found 2 dead male House Wrens inside nest boxes that were being defended actively by unbanded male wrens. One of the dead birds was banded in 1985 as occupant of the box. The back of the head and the upper areas of the back of the dead wren were defeathered and covered with dried blood, and there was a small puncture wound on the back of the head. The second dead wren was found in a box about 2 km from the first one. It was an unbanded male whose back of the head and back were also defeathered and covered with dried blood. In both cases the wrens could not have been dead for more than a few days, as there was no indication of decomposition.

The fact that neither bird was eaten suggests that they were not killed by predators. The defeathered hindhead and back of the dead wrens (apparently characteristic of attacks by small birds, Lombardo 1986), and the presence of a small puncture wound on one of the birds, suggest that a small bird with a sharp, pointed beak was responsible for these killings. Because nest boxes in which we found dead birds were defended by male House Wrens, we believe that male wrens were responsible.

Several observations suggest that House Wrens could kill adult conspecifics. Infant killing by House Wrens has often been observed (Belles-Isles and Picman 1986b), and Beckwith (1913) described a case of heterospecific adult killing during which a House Wren inflicted fatal wounds to a House Sparrow's (*Passer domesticus*) head and back.

Cavities suitable for nesting are probably limiting in our area (Belles-Isles and Picman 1986a). The removal of 23 randomly selected boxes in 1986 coupled with strong site tenacity exhibited by male House Wrens (unpubl. data) may have intensified wren competition for nesting sites and resulted in these two cases of adult killing.

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Possible long-distance pair migration in *Cyanerpes cyaneus*.—Greenberg and Gradwohl (1980) found Canada Warblers (*Wilsonia canadensis*) associating in male-female pairs on migration in Panama, without knowing if the pairs formed locally or not. Similarly, I have often seen male-female pairs of tanagers (Thraupinae) wandering locally in the nonbreeding season in the interior of southeastern Brazil. Here I report possible long-distance pair migration for a thraupine bird, the Red-legged Honeycreeper (*Cyanerpes cyaneus*).

On 18 August 1985, I found a pair of Red-legged Honeycreepers (*C. cyaneus*) probing in flowers atop a eucalyptus at the lake of the Horto Florestal, Rio Claro, São Paulo, Brazil (22°25′S, 47°31′W, 590 m elevation). The male was in winter plumage, although a few dark feathers on body and head suggested that he was regaining summer plumage. On 27 July 1986, a pair of Red-legged Honeycreepers was in the same tree, which had started to flower in June, but had only reached full flower in the crown in late July. The male was in winter plumage, with bright red legs, black wings and tail, and green body.

Apparently, these are the only records of this species for the state of São Paulo. Since 1975, Yoshika Oniki and I have been searching throughout the state for birds, without otherwise finding the species. The nearest known breeding grounds are in eastern coastal Rio de Janeiro, nearly 600 km airline east of Rio Claro (Sick 1985). Sick records wandering birds as far west as the city of Rio de Janeiro, 440 km east of Rio Claro.

The species is known to wander in nonbreeding groups (Skutch 1954, Moynihan 1962), but pair association within these groups has not been confirmed. It seems unlikely that a male and female would separately find a tree so far from the known range of the species in two separate years. It also seems unlikely that an unmated pair would wander together for such distances. I suggest that at least one of the birds was the same in both years, and that this was a case of long-distance pair migration. Long-distance homing to a flowering tree would be interesting, especially as Skutch (1954) and Dickey and van Rossem (1938) consider the Red-legged Honeycreeper a local migrant, while the A.O.U. Check-list (1983) refers to it as a "resident" species. Winter movement to the southern Brazilian highlands is also unexpected, for the birds were in a region colder than anywhere in their known range.

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First report of the nest and young of the Variegated Antpitta (*Grallaria varia*).—While conducting a study on microhabitat use by birds, I found a nest with two young of the Variegated Antpitta (*Grallaria varia*) 80 km north of Manaus, Amazonas, Brazil (2°25′S, 59°50′W). I am unable to find any previously published description of the nest and young of this species. The nest was in upland forest about 25 m from an extensive area of 10–15-month-old second-growth, which had resulted from the clearing of the forest for cattle ranching. After the trees were cut, however, the area was abandoned. After the cutting, human activity had dropped to a minimum, except for an infrequently used trail that passed within 1 m of the nest.

The nest was discovered 19 June 1984 by my field assistant, Jairo Miranda Lópes, on an upright <2-m rotting stump 40–50 cm in diameter. The nest, which was about 1.5 m above the ground, was a shallow cup 20 cm in diameter, lined with a thick mat of very small brown twigs and rootlets, and well concealed by a palm frond. The nest contained two young (eyes open, covered in black down, and spotted with brown juvenal feathers). Their gapes were yellowish, and their mouth-linings were bright red. Voucher photographs of the nest and the young have been deposited in VIREO (V06-1-016, V06-1-017).

In spite of repeated efforts to observe the parents feeding the young, the adult birds were never seen approaching the nest, although they flushed several times nearby. Both were mist-netted (banded and released) several times within 50 m of the nest. I checked the nest every 2 h daily. The young disappeared on 22 June, some time between 10:00 and 12:00 h, leaving the nest intact. It is not clear whether the young fledged, fell out of the nest, or were preyed upon. Lópes and I searched but could not find them. This was also the last day that the adults were captured.

Judging from a recent review of the nests of the members of the subfamily Grallariinae (Wiedenfeld, Wilson Bull. 94:580–582, 1982), the nest described here is typical. Most nests reported contained 2 eggs, were built above ground, but below 3 m, and on top of fallen logs (Wiedenfeld 1982). The young of *G. varia* resembled those of *G. guatimalensis* (Miller, Univ. Calif. Publ. Zool. 66, 1963), except that *G. guatimalensis* nestlings had orange-yellow mouths and gapes. Similarly, the hatchlings of *G. perspicillata* described by Skutch (Life histories of Central American birds, III, Cooper Ornithological Society, Berkeley, California, 1969) were dark-skinned (they were still featherless) and had orange mouth-linings. Although dark-skinned nestlings are the rule in the Formicariidae (Skutch 1969), the color of the mouth-lining and gape seems to vary somewhat. Whether this variability is species-specific or age dependent remains to be determined.

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Project (World Wildlife Fund—U.S. and Instituto Nacional de Pesquisas da Amazonia—Brazil). I thank G. R. Graves, J. V. Remsen, Jr., and D. A. Wiedenfeld for their critical review of the manuscript.—Carlos E. Quintela, *Dept. Biological Sciences, Univ. Illinois at Chicago, Chicago, Illinois 60680.* (Present address: *Museum of Zoology and Dept. Zoology and Physiology, Louisiana State Univ., Baton Rouge, Louisiana 70803-3216.*) *Received 24 Nov. 1986, accepted 12 Feb. 1987.*

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Hammond's Flycatcher (*Empidonax hammondii*) new to Maryland and the Atlantic Coast.—During examination of study skins of Least Flycatchers (*E. minimus*) at the U. S. National Museum of Natural History (NMNH) in August 1986, I discovered an immature female Hammond's Flycatcher (NMNH 479689: mass 8.5 g, unossified skull, little fat, ova to 2 mm, yellow mouth lining) taken 9 October 1963 at Ocean City, Maryland. The bird had been netted by Chandler S. Robbins, who (pers. comm.) collected it because he was not able to identify it in the field. Subsequently, the bird was identified by Lester L. Short as a Least Flycatcher and was deposited with that species.

The specimen's gray throat and chest and quitc yellowish belly—characters that help to identify *E. hammondii* in autumn—and its small narrow bill led me to believe it was *hammondii*. Its flattened wing measured 63 mm, tail 59 mm, tail notch over 2 mm, exposed culmen 12.3 mm, and width of bill at nares 4.5 mm. Its wing formula included 10th primary barely longer than 5th. A few days after this discovery, I took the specimen to the Denver Museum of Natural History (DMNH), where its identity as *hammondii* was corroborated by Allan R. Phillips (pers. comm.).

To my knowledge there are just four other records of this species east of the Great Plains: an autumn specimen from Louisiana (Louisiana State University Museum of Zoology [LSUMZ] 121700; imm. ♂; 27 October 1984; Cameron Parish, Garner Ridge, 3 mi W of Johnsons Bayou School; T. S. Schulenberg [Am. Birds 39:66, 1985]) and winter specimens from Louisiana (LSUMZ 22057; ♀ with no skull ossification data; 17 January 1957; Rapides Parish, Woodworth [=10 mi S of Alexandria]; M. B. Meanley, Jr. [Lowery, *Louisiana Birds.* Third ed., Louisiana State Univ. Press, Baton Rouge, Louisiana, 1974]), Pennsylvania (The State Museum of Pennsylvania [SMP] B1103; imm. ♀; 23 December 1966; Lehigh County, Schnecksville; D. S. Heintzelman [Heintzelman, Auk 85:512, 1968]), and, most recently, Delaware (Delaware Museum of Natural History 76370; ♀ with skull 75% ossified; 24 December 1986; Kent County, about 1 mi S of Woodland Beach; Keith Russell).

Acknowledgments.—I thank R. C. Banks, M. R. Browning, and J. P. Dean for their help and many kindnesses at NMNH; A. R. Phillips for his counsel at DMNH; J. V. Remsen, Jr., and A. G. Mehring for providing specimen data from LSUMZ and SMP, respectively; C. S. Robbins, M. B. Robbins, and the editor for hclpful comments on this note; and M. B. Robbins for apprising me quickly of the Delaware record.—Daniel D. Gibson, *Univ. Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775.* *Received 10 Oct. 1986, accepted 19 Jan. 1987.*

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An exceptionally tall Eastern Phoebe nest.—On 8 September 1983 I discovered an unusual nest (VIREO No. V06-2-002) of the Eastern Phoebe (*Sayornis phoebe*) inside a shed in Geauga County, Ohio, 2 km north of Middlefield. The nest was 74 cm tall from base to rim, nearly 10 times the height of a typical Eastern Phoebe nest (Van Tyne 1957). Despite its abnormal height, it was of standard phoebe composition, made of mud, moss, and grass (Harrison 1975) and was attached to a vertical plywood wall above a passageway connecting two rooms of a shed used for maple syrup production. The nest had an air-dried weight of 970 g, and its cup held the mummified remains of one half-grown phoebe nestling. The nest was measured, photographed, and removed from the wall and is now in the nest collection of the Carnegie Museum of Natural History in Pittsburgh, Pennsylvania.

The base of the nest was 2.4 m above the shed's dirt floor, and the rim was 0.4 m below the shed's sloping ceiling brace. According to the owner of the shed, the nest was built entirely during the 1981 nesting season, and it was used each summer through 1983 without noticeable addition of material. Subsequent examination of the nest revealed an unlayered structure apparently built from a single mud source, embedded its entire length with interwoven moss and grass. The nest was only wide enough (13.3 cm) for a cup (7.0 cm) at the top. Harlow (1912) described an Eastern Phoebe nest with 6 distinct stories, and Smith (1905) reported one with 5, measuring 22.5 cm in height. Weeks (1977) described 3 aberrant phoebe nests with greater than normal dimensions, but these did not involve nest height.

Because the Eastern Phoebe is frequently victimized by the Brown-headed Cowbird (*Molothrus ater*) (Klaas 1970) and will sometimes build a new nest on top of an old one in order to cover over cowbirds' eggs (Bendire 1895, Burtch 1898), the nest was x-rayed (using a GE 100 Dental X-ray, Model 11HHSA1 at 50 kVp and 10 mA) to determine whether cowbird parasitism caused the aberrantly tall nest. Neither buried eggs nor egg fragments were detected in the x-rays, whereas control eggs placed behind the nest produced strikingly clear images.

The tallest phoebe nest previously reported was 38 cm, and it was also of single-season construction (Van Tyne 1957). Van Tyne (1957) speculated that this example of exaggerated nest-building behavior was caused by the birds' "urge" to have their nest rim close to the overhanging ceiling that was a considerable distance above the shelf giving the nest its initial support. This might also account for the nest I found. In the present instance, the phoebes gained initial nest support by using the only substantial projection on the wall, a metal wire fastened 1.2 m below the overhanging ceiling brace. Perhaps in both instances the birds were torn between opposing preferences. The first of these would be the need to attach the nest to some projection or surface irregularity in order to reduce the risk of nest dislodgement, and the second would be the need to have the rim of the nest as close underneath a protective overhang as possible. Regarding the former preference, both Graber et al. (1974) and Weeks (1979) state that falling nests are a significant mortality factor in the Eastern Phoebe, and Jackson and Burchfield (1975) demonstrated the importance of projections on vertical surfaces as nest-attachment sites in another species of adherent, mud-nest builder, the Barn Swallow (*Hirundo rustica*). Regarding the latter preference, the Eastern Phoebe historically nested along stream banks with rocky outcroppings (among other places) and continues to do so today (Tyler 1942, Weeks 1978). At such relatively exposed sites, any mud nest not placed close beneath some protective overhang would be vulnerable to destruction by rain.

An alternative explanation for the nest might be that the phoebes were responding to an artifically raised substrate level beneath their nest. During early spring sugaring activities, a wagon with a 1m-high bed was often placed beneath the passageway where this nest was built (E. Byler, pers. comm.). Perhaps, just as the phoebes had begun construction of this

nest, and therefore were strongly attached to the site, the wagon was parked, effectively raising the substrate level beneath their nest by 1m and stimulating them to construct an exceptionally tall nest in order to maintain their preferred nest-cup height, well above the reach of ground-dwelling predators.

If either explanation is correct, what at first appears to be an example of maladaptive nest building, because of the wasted time and energy required to build such an exaggerated nest, might actually be an expression of adaptive behavior.

Acknowledgments.—I thank H. Weeks, J. Jackson, K. Parkes, K. Bildstein, two anonymous reviewers, and W. Parker for helpful suggestions on an earlier version of this manuscript. I also thank E. Byler who gave permission to collect this nest from his shed, and J. Wallace who generously donated his time and equipment by x-raying the nest.

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ORNITHOLOGICAL LITERATURE

CHECK-LIST OF BIRDS OF THE WORLD. Vol. 11. By Ernst Mayr and G. William Cottrell (eds.). Museum of Comparative Zoology, Cambridge, Massachusetts, 1986:xii + 638 pp. $75.00.—When the late James Lee Peters published the first volume of his check-list of birds of the world in 1931, he could hardly have anticipated that the series would not be completed for 55 years. (Another volume is, in fact, planned, but it will be an index to the entire 15-volume work.) With the publication of the long-awaited Volume 11, a brief historical review is in order.

As is well known, Peters lived to see only the first 7 volumes (through 1951) of his check-list. He had asked the late John T. Zimmer, an expert on South American birds, to prepare the manuscript for Volume 8, covering the suborder Tyranni; Dr. Zimmer left only a partial manuscript at his death in 1957, and Volume 8 did not appear until 1979. At the time of Peters' sudden death in 1952, he had completed the manuscripts for the oscine families Alaudidae and Hirundinidae and part of the Campephagidae. The Museum of Comparative Zoology at Harvard University, which sponsored the series, appointed Ernst Mayr and James C. Greenway, Jr. as editors to continue Peters' work. After a hiatus of 8 years, Volume 9 appeared under this editorship in 1960, and Volume 15 followed in 1962. Editorship varied in subsequent volumes. The sequence of publication of these volumes, quite understandably, became a function of the availability of manuscripts rather than of the number of the volume. Responsibility for preparing the manuscripts for the passerine families and subfamilies (and for the nonpasserine orders and families in the revision of Volume 1) was given to numerous authors, most of whom were experts on the group in question. For widely distributed taxa, authorship was often divided on a geographic basis; this is true of the volume under review, in which, in general, Melvin A. Traylor, Jr. was responsible for African taxa within a family or subfamily, George E. Watson for Holarctic and Oriental taxa, and Ernst Mayr for Australasian taxa. Separation of authorship is not always clearcut, however; for example, both Watson and Mayr have initialed footnotes within the account of the single species "*Niltava*" *rufigastra* (pp. 370, 372).

The format of Volume 11, which covers 6 families of the "Old World insect-eaters," is the same as in other recent volumes; there appears to be a useful increase in explanatory footnoting. A scan through the entire volume suggests that proofreading has been improved. The most conspicuous lapsus is the misspelling "SILVIIDAE" on the running heads of pp. 37–65, 85, and 111. A small block of index entries for names beginning with cha- has been misalphabetized on p. 596; I do not know whether there are similar lapsi elsewhere in the index, as I discovered this one only because I was looking up a particular cha- name. In the generic heading on p. 56, the name *Acrocephalus* is credited to Naumann, but the subgeneric heading for *Acrocephalus* on p. 61 is credited (correctly) to Naumann and Naumann.

The major change effected in Volume 11 has to do with classification. In the introduction to the first of the multi-authored volumes (Vol. 9), Mayr and Greenway stated that they had "pledged themselves at the XI International Ornithological Congress at Basel to follow a sequence [of passerine families] recommended by a special committee [of European ornithologists] appointed by the President of the Congress . . . . This is an arbitrary sequence, but not more so than other sequences proposed. It is essentially the sequence that had been used in the 19th century in most of the standard literature." Peters himself had been a strong adherent of the so-called Wetmore classification, which, while certainly just about as arbitrary as the "Basel sequence," was the sequence used in the 20th century in all of the standard literature of New World birds. Even some of the standard literature of Old World birds, such as Bannerman and Sclater's works on African birds, departed from the "crows last"

sequence. The standard 20th-century checklist of Palearctic birds, that of Vaurie (Bds. Palearctic Fauna Vol. 1, Witherby, 1959), follows the Wetmore sequence of passerine families, which the author believed to be "more satisfactory" than the Basel sequence, in spite of the fact that Vaurie was in general strongly influenced by Mayr. The convenience of the "Peters" checklist and its derivatives (such as the Morony, Bock, and Farrand list, Dept. Ornithol., Am. Mus. Nat. Hist., 1975) as a standard reference was such that its sequence was used for arranging collections, files, etc., even by many ornithologists who preferred the Wetmore sequence.

In their introduction to Volume 9, Mayr and Greenway stated presciently, "In view of the accelerating pace of the study of comparative avian anatomy, serology and ethology, it is to be hoped that definite improvements in this sequence will be found in due time." Those disciplines did indeed contribute toward changes in classification it the next several years. In 1959, however, when that statement was written, Mayr and Greenway could hardly have anticipated the advent of DNA hybridization as a method for deducing phylogenies and hence classifications, nor could they have anticipated the impact of discrepancies between morphological data (given first place on their list) and molecular data, currently one of the most stimulating problems in ornithological research. This clash is nowhere better illustrated than in the introduction to the revised edition of Volume 1 (1979), in which Mayr and Cottrell stated that the "analysis of amino acid replacements in macromolecules . . . has already demonstrated *conclusively* [italics added] that the Anseriformes is a side branch of the galliform birds," a strong statement strongly disputed by Olson and Feduccia (Smithsonian Contrib. Zool. 323:6, 1980) on the basis of both the fossil record and the morphology of recent taxa. In the introduction to Volume 11, Mayr and Cottrell wrote, "We do not doubt that the application of new molecular methods will in due time necessitate numbers of changes from the sequence and categorical ranks adopted by us." This statement signalizes their virtual abandonment of morphology, at least in principle, as the primary criterion for avian classification. This is further emphasized by the fact that several "new" (i.e., post-Basel) families or subfamilies in this volume, such as the Acanthizidae and the Eopsaltriidae, are described as being "reasonably well characterized by life history characters and general habitats, [but with] few (if any) diagnostic morphological characters." I consider one of the important lacunae in the present volume to be the absence of references, under the headings for the "new" family-level taxa, to any published attempts to define these groups. Oddly, in one of the references cited under the heading of "Family Eopsaltriidae," Officer (Australian Flycatchers, 1969) firmly states that the Australian "robins" are flycatchers of the family Muscicapidae. For another example, there are two references cited under the heading for the "new" family Platysteiridae. Contrary to Traylor's note, Ames (Bonner Zool. Beitr. 26: 107–134, 1975) did *not* discuss the "position of family," and in the other reference cited (Wolters, Vogelarten der Erde, 3. Lief:235–236, 1977), the author merely lists genera and species under the heading Platysteirinae (as a subfamily of Laniidae!) without any diagnosis. In Traylor's own short note explaining in advance his classification of African flycatchers (Ibis 112:395–397, 1970), he merely listed the taxa to be included in what at that time was to be a subfamily Platysteirinae in a large or Hartertian family Muscicapidae, and stated that their relationships are not with other "flycatchers" but with the bush-shrikes of the subfamily Malaconotinae. The nearest thing to a definition of the taxon consists of statements that this group of genera is homogeneous, consisting of small- to medium-sized "flycatchers," which are confined to Africa and Madagascar and are black and white or black, white, and chestnut *except for two brightly colored, aberrant species.* Without knowing what their "homogeneity" consists of, there is no way here of telling platysteirids from any other small- or medium-sized African or Madagascan "flycatchers" that happen to be black and white; black, white, and chestnut; or brightly colored.

A review of the history of the classification of the "Old World Insect-eaters" within the "Peters" check-list may be useful. The Basel sequence (Mayr and Greenway, Breviora 58, 1956), reproduced exactly (including unitalicized generic names) except for material in square brackets, was as follows:

Muscicapidae
- Turdinae (incl. Zeledonia) [the latter now believed to be a paruline, although this is mentioned nowhere in the "Peters" list]
- Timaliinae (incl. Chamaea)
- Paradoxornithinae
- Polioptilinae (incl. Rhamphocaenus [*sic* = Ramphocaenus] and Microbates)
- Sylviinae (incl. Regulus, Leptopoecile, Lophobasileus)
- Malurinae
- Muscicapinae
- Monarchinae
- Pachycephalinae

The first "Peters" volume to include the "Old World Insect-eaters" was Volume 10 (1964). In general, the Basel taxa were recognized, although the sequence differed. Included were the Turdinae, Orthonychinae (split off from Timaliinae), Panurinae (=Paradoxornithinae of the Basel list), Picathartinae (also split off from Timaliinae), and Polioptilinae.

Volume 12 (1967) dealt only marginally with the "Muscicapidae" (sensu lato), including the Pachycephalinae and, as a genus incertae sedis, the Piopio of New Zealand, *Turnagra*, subsequently shown to be related to the bowerbirds (Olson et al., Notornis 30:319–336, "1983" = 1984).

The remaining groups of "Old World insect-eaters" took almost 2 decades to complete, including as they do some of the most difficult genera of songbirds. While the authors were struggling with their manuscripts, the editors were deciding, particularly on the basis of the DNA hybridization studies of Charles Sibley, to abandon any pretense of adhering to the previously strongly defended Basel sequence. The Old World warblers and true flycatchers now revert to their previous status as the families Sylviidae and Muscicapidae rather than subfamilies of a giant family Muscicapidae; both families become even smaller than their namesakes in the Wetmore classification, as the warblers lose the genera that now comprise the Maluridae and Acanthizidae; the true flycatchers part with the Australian "robins" and their relatives, placed in the family Eopsaltriidae; and the monarchine and rhipidurine "flycatchers" become two subfamilies of the new family Monarchidae.

In view of the discrepancies in classification between this and previous volumes covering the oscines, I would strongly recommend to the editors of the "Peters" check-list series that in their final volume (index and presumably corrigenda), they offer a revised version of what they conceive to be the current optimum classification at least of the passerines, down to the level of tribes, with full documentation of the publications that led them to effect changes from the originally announced classification.

In my reviews of previous volumes of the "Peters" check-list, I have indicated how the classifications in those volumes differed from the 5th edition (1957) of the A.O.U. Check-list. The 6th edition (1983) adopted the then-fashionable giant family Muscicapidae for the whole "Old World insect-eater" complex, admitting subfamilies Sylviinae (including tribes Sylviini, Ramphocaenini, and Polioptilini), Muscicapinae, Monarchinae, Turdinae, and Timaliinae. Of the species included in these groups, only *Regulus*, the Ramphocaenini, Polioptilini, and Turdinae are any more than marginally North American. The only monarchine included is *Chasiempis* of the Hawaiian Islands, and the only nonintroduced timaliine is the Wrentit, *Chamaea*. With the thrushes, babblers, and gnatcatchers (and their

relatives) having been covered in Volume 10, the overlap between the A.O.U. Check-list and Volume 11 of "Peters" is minimal. The only differences I noted involved treating *Cettia diphone* and *canturians* as conspecific rather than as allospecies of a superspecies as in the A.O.U. list, and the failure of Watson in "Peters" to recognize a subgenus *Corthylio* within *Regulus* for the rather distinctive Ruby-crowned Kinglet (*Regulus calendula*).

A few more technical comments can be offered on points that caught my eye as I paged through this volume. On p. 65, Watson states that the name *Sylvia montana,* used by various authors for the warbler currently called *Acrocephalus dumetorum* Blyth, is preoccupied by *Sylvia montana* Wilson, 1812, which Watson equates with *Motacilla virens* Gmelin, 1789 (i.e., the Black-throated Green Warbler). *Sylvia montana* Wilson is the "Blue Mountain Warbler," which has never been satisfactorily identified from either Wilson's plate or that of Audubon of allegedly the same species (Parkes, Nat. Hist. 94(4):88–91, 1985). Watson's identification of it as what is now called *Dendroica virens* is presumably based on the synonymy of Ridgway (U.S. Nat. Mus. Bull. 50, part 2:784, 1902), which assigned Wilson's plate to the Black-throated Green Warbler and Audubon's to Townsend's Warbler, but in both cases *with a query.* I know of no definitive identification of either Wilson's or Audubon's *Sylvia montana,* although Wilson's name does indeed preoccupy the (undated) use of the name for the *Acrocephalus* cited by Watson, even though it is a species inquirendum.

Article 59 of the International Code of Zoological Nomenclature states that a junior secondary homonym for which a substitute name was published prior to 1961 is permanently invalid. I happen to dislike this provision of the Code, as it forces us to use names invented by extreme "lumpers," but I also believe that if we subscribe to a code we follow *all* of it. The late H. G. Deignan, who favored a gigantic genus *Muscicapa,* published a list (Proc. Biol. Soc. Washington 60:165–168, 1947) of "untenable names in the Old World flycatchers" (i.e., secondary homonyms created by the wholesale lumping of genera into *Muscicapa*). Deignan's "*Muscicapa*" is divided among several genera in "Peters" 11, but according to the Code we must continue to use his pre-1961 substitute names even when the species or subspecies is removed from *Muscicapa.* This rule has not been followed by Watson, in a sampling of the secondary homonyms listed by Deignan. (I did not check all 17.)

Reviewers are usually permitted at least one personal observation. It is annoying to any worker to find that the author of a compilation like "Peters" has ignored published work upon which one has spent a great deal of time and effort. Watson overlooked my studies (Nemouria 4:36–40, 1971) of the genus *Cyornis* (which, unlike Watson, I do not lump with *Niltava*), in which I demonstrated that *C. lemprieri* of Palawan and adjacent islands of the Philippines is *not* a race of *C. banyumas,* but belongs in a superspecies with *C. herioti* of Luzon. Similarly, *C. hainana* does not belong near *C. herioti* and *C. pallipes,* but close to *C. rubeculoides,* as long ago pointed out by Delacour (Ois. et Rev. Fran. d'Ornithol. 2:433–435, 1932). In the species *C. rufigastra,* the alleged Palawan subspecies *litoralis* Stresemann, admitted by Watson, is inseparable from *C. r. philippinensis,* and was in fact refuted by its describer (Stresemann and Meyer de Schauensee, Proc. Acad. Nat. Sci. Phila. 88:341, 1936).

All of these inevitable disagreements aside, the authors of this volume are to be congratulated in having produced an invaluable reference work, on a notoriously difficult group of passerines, under trying conditions (for example, Deignan had started work on the Old World warblers for this volume well before his death in 1968). I do want to reiterate my earlier statement that I believe the editors owe us an outline of their current concept of the classification of the Oscines, which cannot be deduced merely by thumbing through the various volumes of "Peters." (*Note added in proof.*—Vol. 16 has appeared since this review was written: It consists of a comprehensive index and a few corrections only.)—KENNETH C. PARKES.

THE SPARROWHAWK. by Ian Newton, illus. by Keith Brockie. T. & A. D. Poyser, Ltd., Waterhouses, England, 1986:396 pp., 24 black-and-white plates, 90 text figs., 63 tables in appendixes. $35.00 (cloth).—Since Ian Newton published "Population Ecology of Raptors" in 1979, he has been considered one of the foremost authorities on birds of prey. His recent book entitled "The Sparrowhawk" solidifies this perception and demonstrates to those of us who conduct research on raptors what can be accomplished with foresight and long-term studies.

In his 14-year study on Eurasian Sparrowhawks (*Accipiter nisus*) Newton has addressed most if not all of the ecological issues that are commonly investigated by raptor biologists. The book is organized into 25 chapters that discuss many topics including nesting habitat, population trends, foraging behavior, diet, reproduction, mortality, and pesticides. In each chapter, the data are presented and discussed in a readable fashion that both professional and amateur ornithologists will appreciate. Figures are used effectively throughout the text to illustrate trends and patterns in the data on sparrowhawks; in addition, exhaustive tables are provided in appendix form so that specific values and sample sizes can be referenced. I found this style very effective and thought it made the text very readable.

In the first three chapters, Newton introduces us to some general background concerning the methodologies of his study, sparrowhawk morphology and natural history, and various aspects of nesting habitat. In Chapter 4, data on the density and spacing of nests are presented. For example, he found that nesting areas in suitable woodlands typically were occupied from year to year, but that differences in the spacing of these nests existed between study areas. The average distance between nests was greater at higher elevations and in areas with greater soil productivity, which he points out influences prey distribution and abundance.

The foraging ranges of sparrowhawks were investigated using radio telemetry (Chapter 5). Range size was found to be smallest and centered on the nest site during the breeding season. Males tended to have ranges that were smaller than females, although the area used for hunting was inversely related to prey abundance. This relationship was clearly illustrated in a food provisioning experiment, in which females breeding on poor territories reduced their foraging range when they were given extra food.

Because sparrowhawks are woodland raptors, there is little information on their hunting behavior and success. In Chapter 7, Newton provides some additional information by describing several hunting techniques that he observed while monitoring telemetered hawks. Not surprisingly, birds comprised the vast majority of their diet (Chapter 8), with large numbers of fledglings taken in the spring and summer. During Newton's study, the prey taken by sparrowhawks varied with area, season, and year; however, the hawks tended to switch emphasis from species to species throughout their breeding season as the prey fledged their respective young.

The breeding season of sparrowhawks in Britain closely coincides with the availability of fledgling songbirds (Chapter 10). In this chapter, Newton documents how the timing of egg laying is affected by climatic factors (e.g., temperature and precipitation). An important contribution in the chapter is the discussion relating female body condition (i.e., weight) to nest attentiveness and clutch size, and how the male's ability to feed the female during this period—when she is dependent on him for food—largely determines the outcome of the breeding effort. Newton also experimentally demonstrated the importance of food supply and female body condition on nesting success by provisioning females with extra food. He found that provisioned birds maintained heavier body weights throughout the nesting season, laid earlier and larger clutches, and fledged more young than females that were limited to food provided by their mates.

Various aspects of the breeding cycle of sparrowhawks are described in detail in chapters 11–16, with each chapter addressing a particular period in the nesting season. The topics

covered include early stages of nesting (Chapter 11), eggs and incubation (Chapter 12), growth of young (Chapter 13), parental care (Chapter 14), postfledging period (Chapter 15), and trends in breeding success (Chapter 16). This information is presented in great detail and clearly represents a tremendous amount of work over an extended period of time. Anyone working with accipiters or woodland raptors in general will have a tremendous appreciation for the data presented in this section of the book.

The last third of the book covers a variety of topics including age and breeding (Chapter 18), molt (Chapter 19), dispersal (Chapter 20), territoriality (Chapter 21), migration (Chapter 22), mortality (Chapter 23), and effects of pesticides (Chapter 24). One of the most impressive data sets Newton presents is in Chapter 18, where he presents the lifetime reproductive success of 142 female sparrowhawks, and discusses the proximate and ultimate causes of the variation in production that he observed. Clearly, this epitomizes the insight that Newton has demonstrated time and again. His efforts, spanning a 14-year period, should be of particular interest to evolutionary biologists who recently have begun to estimate determinants of fitness using this parameter.

This book will prove to be a valuable reference for those interested in sparrowhawks in particular and biologists interested in raptors in general. I highly recommend it.—MICHAEL W. COLLOPY.

BACHMAN'S WARBLER: A SPECIES IN PERIL. By Paul B. Hamel. Smithsonian Institution Press, Washington, D.C., 1986:128 pp., 7 black-and-white illustrations, $11.95 (paper).—This book is timely. The Bachman's Warbler (*Vermivora bachmanii*) may be extinct, and few people still living have seen it. Indeed, the subtitle of this book may be an understatement. The last nest was found in 1937, the last specimen taken in 1949, the last song recorded in 1958, and the last photo obtained in 1958, although sight records of single birds have continued up to 1980 in the southeastern United States and Cuba.

If you want to find out everything known about the Bachman's Warbler, this is the book for you. Hamel has gathered every possible scrap of information, including references in obscure publications and unpublished correspondence, and he has examined all the specimens in museums, but he has not been able to see the bird in life. Because so few ornithologists have studied this warbler, it is surprising that Hamel found more than 300 study skins in museums and more than 40 eggs.

This warbler has always been a bird of mystery. It was discovered near Charleston, South Carolina, in 1833, and then was not seen again for more than half a century. Later it flourished or was rediscovered in widely scattered swamplands from Missouri southward to Louisiana and eastward to Florida and Virginia, with maximum numbers in the years just before and after 1900.

What happened? This book does not settle that question. Although the references listed here number more than 500, important information about the behavior and requirements of the bird are lacking. The early observers who knew it best were interested mainly in specimens, and the later observers have seen only isolated individuals, often in unexpected situations. The bird was never studied intensively. This lack of knowledge has hindered efforts at preservation and restoration because it has allowed uncertainty about the exact nesting habitat (i.e., whether it was primeval or disturbed forest), although Hamel's case for partially opened forest is convincing to me. The witnesses agreed, however, that the bird bred in hardwood swamps of the South and placed its nest in low bushes.

This report includes an intriguing new suggestion by J. V. Remsen that giant cane (*Arundinaria gigantea*) may have been a key element in the nesting habitat. This plant was

mentioned in virtually all descriptions of nest sites but drew little attention. The dwindling numbers of Bachman's Warblers came at a time when the vast original "canebreaks" were vanishing from the southern wetlands. The soils were fertile for agriculture, and the human settlers virtually eliminated periodic fires and flooding, both favorable to the cane. If Bachman's Warbler was a bamboo specialist, it would be the first such bird named in the United States, although several have been identified in the Neotropics, most of them now very rare. This idea might explain the decline in the Bachman's Warbler when, superficially at least, there seems to be no shortage of wet deciduous forest in the South. The sharp bill and curved culmen of this warbler, unique among the *Vermivora,* suggest a special adaptation to a habitat or way of life.

As a narrow specialist, the Bachman's invites comparison with the Kirtland's Warbler (*Dendroica kirtlandii*), a species that is restricted in breeding season to extensive stands of one plant, jack pine (*Pinus banksiana*), which it does not use directly for nest placement nor for all its foraging, and that winters only in the West Indies. Both species tend to cluster in "colonies" for nesting. Hamel, however, does not take up this comparison nor does he pursue suggestive parallels with the well-studied Golden-winged (*Vermivora chrysoptera*) and Blue-winged warblers (*V. pinus*), which he recognizes as the species most closely related to the Bachman's, nor with the Swainson's Warbler (*Limnothlypis swainsonii*), which was often associated with the Bachman's in southeastern coastal regions.

In groping for an understanding of changes in abundance among migratory birds, biologists usually focus first on problems of the breeding ground, which may be near at hand, and neglect the wintering ground, where the birds spend the greater part of each year. The Bachman's Warbler is the only North American bird wintering exclusively in Cuba. Hamel finds no evidence that the bird occupies a narrow ecological niche in Cuba, but in modern times there has been much clearing of lowlands there for agriculture, and these are the regions we might expect it to favor. Over a longer sweep of time, as Hamel point out, Cuba and the nearby Bahama Islands presented an enormously larger land mass during the Wisconsin glacial period, when the Atlantic Ocean was hundreds of feet lower than at present.

In the years ahead we will be examining sight records warily. Rarity gives a great incentive for self-deception, and enthusiastic bird watchers will be cruising many southern swamps. My experience with the Kirtland's Warbler has sensitized me to this problem. Hardly a year passes without a dubious report, and two of the most convincing narrowly missed being placed mistakenly in the published literature through the good luck of a supplementary cue. In one instance three experienced amateurs had a stunned warbler in hand for comparison with pictures, but when it flew away, it left one feather. In the other instance, a bird was observed at arm's length on shipboard, but fortunately was recorded in a snapshot photo. Neither of these corrective facts might have sufficed for an obscure female *Vermivora.*

On the other hand, a ray of optimism flickers, because this little bird may be missed easily in southern woodlands. Its song is a buzzy trill too high in pitch for many aging human ears and easily ignored by the best of observers among the notes of the abundant Northern Parula (*Parula americana*). It is sufficiently like those of the Golden-winged and Blue-winged warblers that Hamel found these birds responding to playback of the Bachman's song.

More than half of the bulk of this book consists of a comprehensive bibliography, and a listing of published items by subject. Although the volume is slender, it will be used mainly for reference, and a subject index or a detailed table of contents would be useful. Also, a map or a table showing the places and years of occurrence of this bird would have been helpful. The format is unpretentious. The pages appear to have been printed directly from copy prepared on a word processor and the lines are not justified, but consequently, the price has been kept low.—HAROLD F. MAYFIELD.

ESKIMO CURLEW: A VANISHING SPECIES? By J. B. Gollop, T. W. Barry, and E. H. Iversen. Special Publication No. 17, Saskatchewan Natural History Society, Box 1121, Regina, Saskatchewan S4P 3B4, Canada, 1986:159 pp., 7 maps, 23 numbered text figs., 7 tables, 5 appendices. $9.00 (Canadian).—One hundred years ago the Eskimo Curlew (*Numenius borealis*) decreased from being one of the commonest birds in North America to one of the rarest. Consequently its ecology is poorly known. The obvious question, posed in the foreword to this book, is why hasn't the Eskimo Curlew received more attention before from ornithologists. The authors intended to rectify this by compiling all available information on the Eskimo Curlew, including current status, distinctive field marks, life history, and former distribution, among other things. Largely by using quotations from hunters, collectors, and ornithologists who knew the species firsthand, they have put together a sketchy, although complete as possible, story of this species' decline. Many of the quotes come from the time just prior to and during the rapid decline of this curlew. The extent of literature review is truly impressive.

The first 41 pages of this book survey the current status, field identification, history, and natural history of the Eskimo Curlew. The introduction describes the purpose, design, basis of information, and structure of the book. The section on current status includes a table and comments on recent sightings. The species has been seen 25 times in the past 40 years; mostly as singletons or in pairs. Twenty-three birds seen in Texas in 1981 are encouraging, but analysis of the table does not indicate a steady increase over the years. Of particular interest is an account of the egg and skin collections of Eskimo Curlews in the Northwest Territories from 1862 to 1865 by Roderick Ross MacFarlane (to whom the book is dedicated) and of extensive searches for breeding Eskimo Curlews in the same area by one of the authors a century later. No new nests have been found.

The section on field identification contains pointers intended to encourage more careful examination of curlews and to facilitate accurate identification of the Eskimo Curlew. They include photographs and drawings of the Eskimo Curlew, Little Curlew (*N. minutus*), and Whimbrel (*N. phaeopus*), but the dark photograph of the last species hinders comparison. An important error is that the legend for the front views of curlews (Fig. 6) is incorrect. The sequence from left to right should read: Eskimo Curlew, Little Curlew, and Whimbrel. A photograph compares an Eskimo Curlew egg with those of the Whimbrel and Long-billed Curlew (*N. americanus*). The authors think that identifications of Eskimo Curlews were probably more reliable when the species was abundant. Of the three main field guides, the authors rate the one published by National Geographic as the most useful for identifying the curlew.

The next section on life history summarizes the annual cycle (breeding, migration, winter), habitat (shown also in photographs throughout the book), food and feeding habits, other behavior, and hunting and decline of the species. Maps show the Eskimo Curlew's distribution (sightings and probabilities) and migratory routes in North and South America. Another shows the North American range of the crowberry (*Empetrum nigrum*), an important food of the Eskimo Curlew.

The last 66 pages of the text detail the Eskimo Curlew's status, dates of occurrence, and distribution region by region throughout North and South America. It is mostly organized by seasons—breeding, fall migration, winter, and spring migration—followed by a short list of records of North American stragglers. This section would have been improved by moving the long quotations to the section on life history.

Additional tables and appendixes present the scientific names for Eskimo Curlews over the years, the common names used in different regions, and the dates and numbers of Eskimo Curlews encountered in Labrador (1770–1786) and on "big flight" years along the Massachusetts coast (1808–1888). This book is ornamented by a section on "Glimpses (short

telling quotes) of the Eskimo Curlew" and another on the "Last of the Curlews," a 1954 Canadian novel later turned into an animated children's movie.

Some minor problems in this book are lack of an index; no guidance in the text to find maps; and reliance, despite the authors' admission of insufficiency, on clutch collections to estimate annual abundances. A more significant shortcoming is that, while the authors do achieve their goal of compiling what is known about the natural history of the Eskimo Curlew, they did not attempt to synthesize that information and draw some conclusions about the Curlew's demise. Reading between the lines, it appears that constant ubiquitous hunting, facilitated by flock tenacity and habitat destruction have led to the near extinction of this bird. But other shorebird species were decimated a hundred years ago and have partly recovered. Why hasn't the Eskimo Curlew? Can understanding of the history of this once abundant, now rare bird help us foresee and forestall problems for other species?

I enjoyed this unusual and eclectic book. The story of the Eskimo Curlew is dramatic. The authors tell it with the records of hunters, collectors, and biologists as well as the creations of writers, photographers, and artists. I believe that not only biologists interested in shorebirds will find this book informative, but any biologist interested in populations and in conservation of species, particularly threatened ones, will find this book instructive and worth acquiring.—ELIZABETH P. MALLORY.

STATUS AND CONSERVATION OF THE WORLD'S SEABIRDS. By J. P. Croxall, P. G. H. Evans, and R. W. Schreiber (eds.). ICBP Technical Publication No. 2, ICBP, Cambridge, England, 1984:x + 778 pp., 111 figs. and maps, 92 tables. £24.90.—This volume resulted from the ICBP 18th World Conference in 1982, and should rank among the most useful books about birds to have appeared during recent years. The 80 authors, representing about 50 institutions, present the latest information on populations of the world's seabirds. The 95 pages of references—including many citations in languages other than English—and the information contained in numerous tables and figures should be of use to tourists interested in natural history, conservationists, resource managers, zoogeographers, ornithologists, and ecologists. All zoological libraries and anyone interested in birds or bird conservation should acquire a copy.

The "Editors Introduction" provides a world map and species table that allows one to locate information on any of the 282 seabird species addressed. The species treated do not include birds of inland seas or marshes (e.g., Ciconiiformes; some terns, cormorants, and pelicans) nor nearshore "seabirds" such as sea ducks, grebes, loons or waders, and as one might expect in a volume such as this, the depth of treatment varies from chapter to chapter. For example, the status of seabirds in the Falkland Islands is discussed in 22 pages, compared to 14 pages for the whole of the USSR and 11 pages for China. This, of course, could not really be avoided, and to have what information is presented, for many areas which we rarely hear (or read) about, represents a commendable effort. Only the western Canadian Arctic, a part of Antarctica, the east coast of South America, and the west coast of "mainland" Mexico are not covered in the volume; all or most of the "seabird" areas of the world, however, are included.

For those geographic areas treated, 38 chapters contain a review of the available information on population trends, present population sizes, breeding localities, conservation-management problems, and recommendations for management and further work. Four additional chapters discuss conservation issues in general, including effects of feral animals, human exploitation, fisheries conflicts, and breeding habitat destruction; four others discuss specific examples of these problems.

The last chapter, contributed by the "ICBP Seabird Specialist Group," might appear to

be a summary of the priorities for seabird conservation and associated research discussed in the preceding chapters. In many ways it is, but it suffers from an apparent avoidance of political issues. Among the preceding chapters, three were written almost entirely about the tremendous, negative direct impacts that gill netting has had or is having on populations of diving seabirds, to say nothing of indirect effects, as this activity alters nearshore marine communities. In addition, virtually every other chapter that treated a species of diving seabird also identified gill netting as a problem. Nevertheless, the summary recommendation (p. 775) identified only two species of penguins, and a few seabird colonies in eastern Canada as being affected enough that concern would be justified! Truly, this is not the case (as many chapters illustrate) and the mortality caused by gill netting flies in the face of several international treaties. (The Migratory Bird Treaty between the U.S. and several other countries is one example.) Another case of how summary recommendations seemed to have avoided "rocking the boat" is in regard to Antarctica. Various chapters identify dramatic changes in seabird colonies caused by human activity, and also identify other, near-certain changes that will result from proposed development, all of which are already "prohibited" by international treaty. Although most of the recommendations contained in this chapter seem to me to be well founded, the cursory treatment of these two subjects is perplexing, especially because the chapter contains a section on needs for further "Legal Protection."—David G. Ainley.

Birds of New Zealand and Outlying Islands. By M. F. Soper. Whitcoulls Publishers, Christchurch, New Zealand (obtainable in the U.S. from International Specialized Book Services, Inc., 5602 NE Hassalo St., Portland, Oregon 97213), 1984:216 pp., 196 color photographs by the author, 2 range maps. $29.95 (U.S.).—This is a welcome addition to New Zealand's books on birds, in this case another by Dr. M. F. Soper, a proficient writer and skilled bird photographer. The book covers 305 species including extralimitals on outlying islands as far north as Norfolk and Raoul and as far south as Macquarie. Two full-page, labeled maps preceding the introduction to the book show the extent of the area covered.

The text is in sections, each constituting an order of birds. Within the sections each family of birds is first described in a box, then followed by an individual listing of each species with pertinent comments on its habitat, appearance, and behavior. The boxing of each family of birds prior to the listing of its species is a helpful feature.

I have one criticism of the book's organization. The 196 photographs, all in full color and superb, are in eight clusters, none included in the pagination. In each cluster there may be anywhere from one to eight photographs per page. Although the photographs are numbered from 1 to 196, and referred to from the text, I found no easy way of knowing in which cluster to search for the number I wanted. To see the picture of the particular species, I had to locate the cluster and then turn the pages in the cluster for the number.

Of moderate size (6 × 9 in.), this book makes a fine companion to "The New Guide to the Birds of New Zealand" by R. A. Falla, R. B. Sibson, and E. G. Turbott (Collins, 1979). Anyone taking a trip to New Zealand, or to the islands in its vicinity, should include both books, as their texts and illustrations supplement each other nicely.—Olin Sewall Pettingill, Jr.

Birds of the Cayman Islands. By Patricia Bradley, with photography by Yves-Jacques Rey-Millet. Published by P. E. Bradley, Box 1326, George Town, Grand Cayman, Cayman

Islands, British West Indies, 1985:245 pp., 72 color photographic illustrations, 7 maps, quarto, no price listed but less than $30.00 U.S.—The three Cayman Islands lie in the Caribbean 240 km south of Cuba and 280 km northwest of Jamaica (the smaller Cayman Brac [38 km^2] and Little Cayman [25 km^2] are ca 120 km east of the larger Grand Cayman [263 km^2]). They are low (maximum elevation 44 m) islands of coralline limestone astride a submerged ridge northwest of the 6000-m deep Cayman trench. Their isolated location has contributed to their importance ornithologically. They comprise a landfall and wintering site for ca 120 North American migrants and are home to 45 breeding species, several of which winter elsewhere (e.g., Least Tern [*Sterna antillarum*], Black-whiskered Vireo [*Vireo altiloquus*], and Gray Kingbird [*Tyrannus dominicensis*]).

Many of the permanent residents exhibit in combination a variety of adaptive responses to remote island life (e.g., simplified song, short-rounded wings, small clutch size, large beaks) in comparison to close relatives on the mainland or Cuba. Not all endemics, however, follow the ecogeographic "rule" of overall larger body size. In fact the West Indian Woodpecker (*Melanerpes superciliaris*), Northern Flicker (*Colaptes auratus*), and Yucatan (*Vireo magister*) and Thick-billed (*V. crassirostris*) vireos, to mention a few, are substantially smaller than congeners on other islands or on the mainland.

Now Patricia Bradley has made these and other interesting Cayman birds accessible to the general public with an attractively executed field guide that provides succinct baseline information for a meaningful birding-research reconnaissance of the Islands. The book begins with a Foreword by Prince Philip in which he endorses both birding and nature conservation. Next, in the Preface, Oscar Owre entreats the user to observe birds carefully and thoughtfully in the Caymans. In the first part of the Introduction the author lists goals which have resulted in the present publication. Following in this section are brief summaries for the Caymans of climate, geography, geological history, origins of the avifauna (following James Bond), breeding birds, endemic subspecies (there are 16), nonbreeding birds, and the four local habitat zones, and birds and plants characteristic of each. Also included are a short essay on status of conservation in the Islands stressing the need for continued vigilance, a figure showing topography of a bird, and a glossary of bird-related terms.

The species accounts, including 57 unnumbered pages of excellent color photographs of resident birds, provide descriptions of diagnostic field characters for all breeding, migrant and transient species having more than casual or accidental occurrence in the Islands. Range, preferred Cayman habitat (complementing data in an earlier section on ecosystems and habitat zones), and habits (e.g., foraging, summering, flying, length of breeding season, clutch size, a phonetic rendition of a typical vocalization, and abundance and distribution of each form in the Caymans) are also covered.

The first of two appendices lists 29 rarities (among them a Swallow-Tanager [*Tersina viridis*]!) not mentioned in the main text, recommended supplemental field guides, and another checklist of breeding birds with the Cayman Islands on which they breed. A selected bibliography of books and papers closing this appendix is a useful feature.

Appendix II addresses "birding" in the Caymans with advice on garb, tips on travel, and a reminder to observers that species new to the islands are always a possibility. The author cautions about care in walking in areas of pinnacled limestone and coastal ironshore—appropriate admonitions I feel, and I speak from experience on Grand Cayman in this regard. Novices should also have been made aware that several species of toxic shrubs and trees (e.g., maidenplum [*Comcladia integrifolia*] and manchineel [*Hippomane mancinella*]) are common on Grand Cayman—a discovery I made with some uncomfortable results in 1971.

A section entitled "Phototips" by Yves-Jacques Rey-Millet, the principal photographer, follows Appendix II. This is an important feature because the writer concentrates on pho-

tographic equipment and techniques suited to the tropical island environment, which is characterized by high humidity, heat, harsh quality of sunlight, and dipteran pests.

Typographical errors are few, mostly words capitalized that should not have been or extra words missed in proofreading. It should be noted, however, that *Icterus leucopteryx bairdi* is mispelled *bardi* on p. 201, and *bairdii* on p. 20.

In the species accounts no mention is made under "Range in the Caribbean" of the occurrence of the Caribbean Dove (*Leptotila jamaicensis*) and the Jamaican Oriole (*Icterus leucopteryx*) on Isla San Andres or of the Thick-billed Vireo on Isla Providencia. In addition, missing for Grand Cayman are a specimen record of the Black-whiskered Vireo (*V. a. altiloquus*) (see Barlow, J. C., Bull. Brit. Ornithol. Club 98:144–146, 1978) and an autumn record of the Bay-breasted Warbler (*Dendroica castanea*) (Johnston et al., Quart. J. Florida Acad. Sci. 34:152, 1971).

Overall this is an excellent little book filled with pertinent information about Cayman Island birds and as such is an important addition to the ornithological literature of the Caribbean. I wish I'd had this guide in 1974 during my field studies on Grand Cayman. I recommend it.—Jon C. Barlow.

The Birds of Wallacea (Sulawesi, The Moluccas & Lesser Sunda Islands, Indonesia). By C. M. N. White and Murray D. Bruce. British Ornithologists' Union Check-list No. 7, 1986:524 pp. £33 (£35 overseas).—The island region between the Asiatic (Sunda) shelf and the Australian (Sahul) shelf has long been a source of controversy among zoogeographers. Two solutions for the treatment of the fauna of this area have been proposed. According to one, a north-south line called Weber's Line, is drawn through the islands. This line separates the western islands (with their prevailingly Malaysian fauna) from the eastern islands (with their prevailingly Australo-Papuan fauna), and is said to be the border between the Oriental (Indo-Malayan) and the Australian regions. The other solution is to combine all the islands between the two shelves into a separate biogeographic region, designated by Dickerson et al. (1928) as Wallacea. It includes four rather different island regions, (1) the Philippines, (2) Sulawesi (Celebes) and adjacent islands, (3) the Lesser Sunda Islands, and (4) the Moluccas. The Philippines are often excluded from Wallacea, although definitely included by Dickerson et al. when they coined the term.

The other three regions up until now have been rather poorly dealt with by avian faunists, and we ornithologists owe a great debt of gratitude to the late C. M. N. White and to Murray D. Bruce for having now given us an excellent avifauna of this region, based on an exhaustive study of the literature and the collections existing in European and American museums. Being an island region, it is very rich in endemics; indeed there is hardly an island that does not have its peculiar bird, including many endemic genera, particularly on Sulawesi.

With usually only small series available from any one island, Wallacea was a favorite area for subspecies describers (including this reviewer). White and Bruce critically review all those for which they could get enough material and reject a considerable number of them. Unfortunately they do not list the names they consider as synonyms. From the tentative nature of many of their conclusions, it is evident that a great deal of work is still to be done in this region.

The systematic list of the 524-page volume covers 347 pages; the remaining 177 pages are devoted to a long introduction, consisting of a discussion of the geography (five detailed maps), vegetation, biogeography, migration, and history of exploration. Particularly valuable is the detailed analysis of the zoogeography, with a discussion of endemism (lists of endemics) and routes of colonization. A 57-page bibliography gives a gratifyingly complete record of

the literature of the area. Five appendices record contents of recent collections, a gazetteer of the islands, a list of uncertain records, and a listing of all 676 species on the basis of their status (breeding, visitor, rare, etc.).

The publication establishes an indispensable and very reliable foundation for all ornithological research in this area. Murray Bruce deserves our thanks for having undertaken the laborious task of completing a manuscript left unfinished by White at the time of his death and actually largely rewriting it. With good faunas already in existence for all the surrounding regions (Malaysia, Philippines, New Guinea, Australia), the white area (Wallacea) in the faunal maps is now filled most satisfactorily.—ERNST MAYR.

EASTERN BIRDS OF PREY. By Neal Clark. Thorndike Press, Thorndike, Maine, 1983:174 pp., black-and-white photographs. $7.95 (paper).—From the author's introduction: "The purpose of this book is to enlighten and inform readers about the more common diurnal and nocturnal birds of prey found east of the Mississippi River. More than a field guide, this is a collection of background history, natural history, and anecdotes to be read before and immediately after a trip to the woods, and should especially come in handy once a bird has been identified." I have no idea what is meant by "background history" of a bird, but if you wish accurate "natural history" this is not your book. "Anecdotes" abound, many of questionable veracity, and many quoted out of context and misleading to the neophyte.

I cannot recommend this book to anyone. Misleading and undocumented statements and factual errors abound, beginning with the first sentence of the first species account: "The cosmopolitan osprey, or fish hawk, is the only hawk-like bird that dives into the water." At least three species of fish eagles (*Haliaeetus* spp.) plunge into the water after fish (Brown and Amadon, Eagles, hawks and falcons of the world. McGraw-Hill, New York, 1968). The paragraph continues: "It is found on every land mass on earth except New Zealand and Antarctica. Only a decade ago, however, it was in serious trouble, hovering near the brink of extinction." It is true that the Osprey (*Pandion haliaetus*) is accidental in Greenland and occurs in winter in South America but I would not recommend either locality for one wishing to add the species to his or her list. Numbers were considerably reduced in much of North America but the species was hardly near the brink of extinction.

According to Clark, the Sharp-shinned Hawk (*Accipiter striatus*) ". . . is considered endangered in Ontario." In contrast, Peck and James (Breeding birds of Ontario: Nidology and distribution, Vol. 1, Royal Ontario Museum, Toronto, Ontario, 1983) state that: "The Sharp-shinned Hawk is the commonest of the three accipiters in Ontario . . . ." Clark states that the hurricane of 1938 greatly contributed to the overall decline of the sharp-shin in New England, "for scores of known nesting sites were razed by the infamous storm. The species has not yet fully recovered." On the other hand, the Northern Goshawk (*A. gentilis*) "has actually benefitted [sic] by mankind since the 1940's." The causes are that it ". . . feeds lower on the food chain (mammals and game birds, etc.) . . . and, more importantly there's been a gradual spread in New England of mature forest land . . . ." I find it most curious that trees are lacking for one species but not for the other. Goshawk populations have increased, at least the southern limits of their range, but the reasons are obscure. Sharp-shinned Hawk populations may have decreased slightly in the last few years but we lack evidence to document any change.

I could go on for pages, listing errors and misinformation, but I will close with an example of a misleading anecdote contributed by Jack Swedberg, a photographer: ". . . There was one occasion when she [a female Goshawk] really let me have it. She came in and sank her talons into my forehead. She hit me so hard—she was coming at me around 60 miles an

hour [!] and weighed probably two pounds—that she knocked me off my feet." Clark fails to hint, let alone state, that this was nest defense. This, and other lurid anecdotes presented for the species may help to keep children out of the forests and loaded shotguns in the hands of those who must venture into the wild. The only virtues of this book are the price and the few excellent photographs among the many of indifferent quality.—HELMUT C. MUELLER.

BIRDS OF THE TEXAS COASTAL BEND: ABUNDANCE AND DISTRIBUTION. By John H. Rappole and Gene W. Blacklock. The W. L. Moody, Jr. Natural History Series No. 7, Texas A&M Univ. Press, College Station, Texas, 1985:126 pp., 14 color plates, 1 black-and-white plate, 5 maps, 7 numbered black-and-white drawings. $19.50.—Although the Coastal Bend region of south Texas encompasses only nine small counties along the northwest coast of the Gulf of Mexico, with 495 recorded species it is the richest bird country north of the tropics in North America. Because of its geographic position, over 80% of the continent's migrating species pass through the area on their way to and from their wintering grounds. Consequently, only Texas as a whole and the state of California have higher species counts that the Coastal Bend of Texas. It is no wonder that this region is visited annually by thousands of birders on vacation or on "listing" missions, several commercial birding tours, and numerous university ornithology classes on field trips. It is only surprising that such a reference book has not been previously published.

As the title suggests, this volume is designed to present more detailed information on the distribution, abundance, and seasonality of birds in south Texas than is available in current field guides or existing state natural history references. It is not intended as a substitute for identification guides, nor does it contain details of the natural history of each species. In the latter sense, the book differs from most regional or state reference works.

The book is divided into a Preface and seven chapters. The Preface includes an interesting historical account of the contributions of many ornithologists and birders to the avifaunal information about the region. After a short introductory chapter, which describes the general climatic and topographic features of south Texas, the authors describe in the second chapter 14 major ecological communities. The description of each habitat type is accompanied by lists of the characteristic plant and avian species. Plant associations or topographic features typical of each habitat are also illustrated with high-quality color photographs. However, one plate (Plate 2) is obviously mislabeled. A beautiful sunset on the Laguna Madre, a lagoon that separates Padre Island from the mainland, is mistakenly titled as a photograph of the Gulf of Mexico.

The third chapter consists of brief but reasonably thorough accounts of all bird species in the region. This section, which constitutes the bulk of the volume, contains notes on the general status, seasonal occurrence, periods of abundance, breeding periods, and habitat preferences of known specimens. Few sight records are included, but, unfortunately, to obtain information on specimen records the reader must turn to the Appendix, a minor inconvenience. Not all species described in the species accounts, however, are listed in the Appendix. Whereas some species known only from sight records (e.g., Barrow's Goldeneye [*Bucephala islandica*]) are listed in the Appendix with the notation "none" indicating that there are no known specimens; other species (e.g., Harlequin Duck [*Histrionicus histrionicus*]) are omitted. Some specimen records published after 1980 are not included in the specimen documentation.

The final four chapters are relatively short and include brief accounts of bird migration, conservation problems, seasonal checklists (a graphic presentation of occurrence), and locations of major habitat types. Of these, the most useful chapter to most people who are unfamiliar with the area is the latter, which includes instructions for driving to good bird

watching localities in each habitat type. The extensive bibliography provides an index to most papers that document the distribution of birds and history of ornithology in south Texas.

I recommend this book to anyone who intends to study or observe birds in the Texas Coastal Bend. This useful text will assist both birders and professional ornithologists in the exploration and enjoyment of coastal south Texas.—BRIAN R. CHAPMAN.

CONNIE HAGAR: THE LIFE HISTORY OF A TEXAS BIRDWATCHER. By Karen Harden McCracken. Texas A&M Univ. Press, College Station, Texas, 1986:296 pp., 1 black-and-white photograph. $18.95.—Perhaps, some might argue that a biography of a birdwatcher should not be reviewed in a professional journal. But, Connie Hagar was no ordinary birdwatcher. And the book contains more than the remarkable story of an interesting human being; it also contains a wealth of information about the bird life in the Texas coastal region.

Connie Hagar, born to the genteel life of music lessons and tea parties, forsook her social position to become a full-time birdwatcher. Encouraged and supported by an incredibly understanding husband, Jack, Mrs. Hagar made daily trips to observe birds for over 35 years. She documented her observations in a journal and meticulously reported her unusual sightings to prominent ornithologists. As a result of her communications, which included two papers published in "The Wilson Bulletin" and one in "The Auk," she and Jack entertained at their Rockport Cottages literally every important person in the field of ornithology during the 1950s and 1960s. Their small motel became a haven for birdwatchers, ornithologists, and naturalists from all over North America.

The biography is written on two levels. On one level the author portrays the life of Connie Hagar, her love of nature, and her many attempts to share her knowledge with others. On the other level, the book describes the birds that Mrs. Hagar observed and wrote about. Because she saw at one time or another every resident, transient, or accidental species in the Texas Coastal Bend, there is much space devoted to accounts of various species. It is difficult to decide which level is more interesting and they are skillfully blended to make the book both interesting and informative.

The book contains a forward by Roger Tory Peterson, a frequent visitor at the Hagar Cottages. In the forward, Peterson says that "we owe a debt of gratitude" to the author of this book "for putting on record the life story of a remarkable woman who had many friends." I agree.—BRIAN R. CHAPMAN.

THE PRESERVATION OF SPECIES. By Bryan G. Norton (ed.). Princeton Univ. Press, Princeton, New Jersey, 1986:305 pp., 3 tables. $29.50.—In 1981 the Center for Philosophy and Public Policy assembled an interdisciplinary group of biologists, social scientists, attorneys, resource managers, and philosphers and "encouraged them to think broadly, abstractly, and 'philosophically'" about the problem of reduced biological diversity. "The Preservation of Species" is the result of that endeavor. The book presents no new data, nor does it offer a recipe for "solving" the problem; rather it simply, but effectively, presents 11 disparate viewpoints on the issue.

The three biologist-contributors to the volume (T. E. Lovejoy, L. B. Slobodkin, G. J. Vermeij) each provide reasonable, general summaries of (1) the rate of species extinction, (2) the characteristics that make some species more prone to extinction than others, and (3) the link between biological diversity and the quality of human life. Although each of the chapters is well written, there is not much here that most practicing ecologists do not already know. Similarly, a chapter by social scientist S. R. Kellert sheds little new light on what is

needed to effect changes in the way the world's human population perceives the problem of decreasing diversity. These four chapters, along with two modest essays by T. L. Leitzell and R. L. Carlton on management and logistical aspects of the problems, and a lengthy contribution by A. Randall on species triage in an economic setting, however, do provide the necessary backbone upon which the four philosopher-contributors (J. B. Callicott, B. G. Norton, D. H. Regan, E. Soba) hang the meat of this offering: the value (anthropocentric and intrinsic) of biological diversity. I especially enjoyed these four chapters, not only because of their insightful didactics, but also because of the juxtaposition of their arguments. The latter, especially, challenged me to reformulate my thoughts on the issue, while the former enabled me to do so with newfound logic.

The four philosophical chapters provide a broad spectrum of views on the value of individual species, both natural and unnatural (i.e., domestic), and they pose a number of thought-provoking, hypothetical "last person" questions that address our options regarding biological diversity in a less-than-perfect world. For example: Should our attention be focused on saving individual organisms, species, or ecosystems? Should we admit the need for triage; and, if so, what criteria should we use? In our attempts to maintain biological diversity in a changing world, how much emphasis should be placed on stability? And what, if anything, should be stabilized? Should we attempt to stabilize the number of individuals in a population, the number of populations in an ecosystem, or the number of ecosystems? How important is the supposed dichotomy between what is natural and what is artificial? Does the rarity of an object increase its value regardless of its naturalness? Should our own extinction be viewed as a necessary preamble for the evolution of a more intelligent group of organisms? These and other questions create fertile grounds for philosophical discourse on the issue, and the book will make for fine reading in graduate seminars.

Although the book is thick with references to Charles Darwin, Paul Ehrlich, Aldo Leopold, and Norman Myers, the most common thread throughout the contributions is our obscene lack of information regarding the biological diversity of our planet. There is a growing realization among ecologists that we simply do not possess the information necessary to make reasonable recommendations for the conservation of biological diversity (cf. Mares, Science 233:734–739, 1986). Thankfully, "The Preservation of Species" is not only an *insightful* book, it is an *inciteful* one as well. We can only hope that the current offering, along with other recent efforts such as E. O. Wilson's "Biophilia" (Harvard Univ. Press, Cambridge, Massachusetts, 1984), will be read widely, and that the scientific community and responsible governments both will respond to the urgent need to collect data on the ecosphere's biological diversity.—K.L.B.

DISTRIBUTIONAL CHECKLIST OF NORTH AMERICAN BIRDS. VOLUME I. UNITED STATES AND CANADA. By David DeSante and Peter Pyle, illus. by F. P. Bennett, Jr. and Keith Hansen. Artemisia Press, Lee Vining, California, 1986:xiii + 422 pp., 51 black-and-white drawings, colored cover. $30.00.—It was one of the Gilbert and Sullivan characters, I believe, who sang a song called "I've got a little list." Most birders that I know, even some hard-core professionals, keep some sort of bird lists. Many people have several such lists, often of esoteric nature. But the mechanical effort of keeping such lists can get to be overwhelming. This elaborate and attractive publication gives us a list to end all lists and also makes the keeping of lists easier.

The authors offer three objectives for their work: provide a compendium of state and province bird lists developed from uniform criteria; provide a convenient means for bird-watchers to keep their North American and state life lists; and most importantly, provide up-to-date status and abundance classifications for the birds on these lists.

The book is in the form of a giant matrix with over 60,000 cells (66 geographical units × nearly 1000 species). Of course about half of these cells contain no information. In the introduction the authors tell us that as of 28 February 1985 there were "28,031 potential 'ticks'" (cells containing information). The area covered is continental North America north of the Mexican border, including the Hawaiian Islands, but excluding Greenland. For each species in each state list a terse coded status is given. Thus in Wisconsin the American Black Duck (*Anas rubipes*) is fS, uW (fairly common in summer, uncommon in winter). The code symbols are fully explained in the introduction and the abundance categories are defined carefully and quantitatively. Above this information in the cell is a blank space that can be used as the owner of the book desires.

The distributional information is probably as accurate as can be attained at the time of the closing date of the publication. The authors assembled the first drafts of the state lists from the 1957 A.O.U. Check-list and then against the 1983 list when it became available. These preliminary lists were then circulated to at least two reviewers from each state who carefully checked the status. Over 150 people were involved in this process. The revised lists were then checked against current information in "American Birds." For each state, a list of problem species was then recirculated to the local reviewers for final consideration. There may be some instances where one might disagree with the status classification given, but as bird distributions and populations are not static things, such disagreements are inevitable as time passes and the present number of these should be small. It is intended that the classifications are representative of the time period 1975–1984. Species that have been unrecorded in the last 50 years or species that have not bred for the last 10 years are so indicated.

There are indeed two lists: "Native Populations" and "Introduced Populations." The rationale for this separation is rather vague. In West Virginia, as in much of the Middle West, the European Starling (*Sturnus vulgaris*) and the House Finch (*Carpodacus mexicanus*) have about the same status as the Northern Cardinal (*Cardinalis cardinalis*). All three entered the state from ranges outside the state, unaided by man. That the first two have come within the memory of those living and the last came shortly after the retreat of the Pleistoscene glaciers makes little difference. Indeed, the starling is now a very important component of the avian community, particularly in the winter.

Each new segment of the book is graced by an attractive black-and-white sketch by F. P. Bennett, Jr. or Keith Hansen of one of the birds in the segment. Some of these show poses not usually shown as, for example, the head-on view of a Whip-poor-will (*Caprimulgis vociferous*) chasing a moth.

Volume II, which will cover the rest of the area of the 1983 A.O.U. Check-list, Mexico, Central America, and the West Indies, is still to come.—George A. Hall.

Audubon Reader: The Best Writings of John James Audubon. By Scott Russell Sanders (ed.). Indiana Univ. Press, Bloomington, Indiana, 1986:245 pp. $29.95 (cloth), $9.95 (paper).—This collection of John James Audubon's writings includes 15 selections drawn from his 60 "Episodes," 16 of the approximately 500 bird descriptions from the "Ornithological Biography," and selections from his letters and journals. Audubon's "Episodes" are interludes scattered among the species discussions of the "Ornithological Biography," which were meant to describe American "scenery and manners" and to relieve the boredom he imagined his mostly wealthy readers might experience while reading the bird descriptions. Editor Sanders' main purpose is to show that Audubon's writing is worthy of consideration as good literature. In his excellent introduction to the collection, he compares Audubon's work favorably with the most influential nineteenth century authors, among

them Washington Irving, James Fenimore Cooper, Herman Melville, and Henry David Thoreau. Sanders emphasizes Audubon's place in the "distinguished American band of roving nature reporters" including him with Mark Catesby, the Bartrams, Alexander Wilson, Thoreau, John Muir, and Aldo Leopold. He admires Audubon's colorful language and his "fearless, passionate, indefatigable presence" in his works. Sanders reminds us that Audubon was more than a marvelous artist and scientist, and that he deserves recognition as an accomplished literary figure as well. The selections he presents show the variety of Audubon's experiences and Audubon's growing concern for man's impact on the abundance of wildlife present at the time. Sanders also explores the impact of Audubon's editors, especially the destructive censorship of his granddaughter, Maria, on his published work. Although many of the selections are familiar to readers of Audubon, Sanders succeeds in putting them in a fascinating new light.—Albert R. Buckelew, Jr.

BRIEFLY NOTED

Proceedings of the Bird and Man Symposium Held in Johannesburg 10–15 April 1983. By L. John Bunning (ed.). The Witwatersrand Birds Club, P. O. Box 72091, Parkview 2122, Johannesburg, South Africa, 1985:361 pp. $32.00 U.S.—Thirty-one papers, 8 posters, and a "keynote" lecture on The Effect of Man on the Britsh Avifauna by C. M. Perrins were given at this symposium. Unfortunately, 9 of the papers are represented in this volume only by a brief Summary. The topics range widely and, while most of the papers deal with African birds, there were a few participants from the U.S. and Australia.—G.A.H.

A Review of the Problem of Lead Poisoning in Waterfowl. By Glen C. Sanderson and Frank C. Bellrose. Special Publication No. 4, Illinois Natural History Survey, Champaign, Illinois, 1986:34 pp. (No price given.)—G.A.H.

Bird Damage to Ripening Field Corn Increases in the United States from 1971 to 1981. By Jerome F. Besser and Daniel J. Brady. Fish and Wildlife Leaflet 7, U.S. Fish and Wildlife Service, Washington, D.C. (obtainable from Superintendent of Documents), 1986: 6 pp. (No charge.)—G.A.H.

Checklist of the Birds of Belize. By D. Scott Wood, Robert C. Leberman, and Dora Weyer. Carnegie Museum of Natural History Special Publication No. 12, Pittsburgh, Pennsylvania, 1986:22 pp. $2.00.—Lists 470 species known for the region in "checklist" format and gives a coded status of each in 6 ecological areas.—G.A.H.

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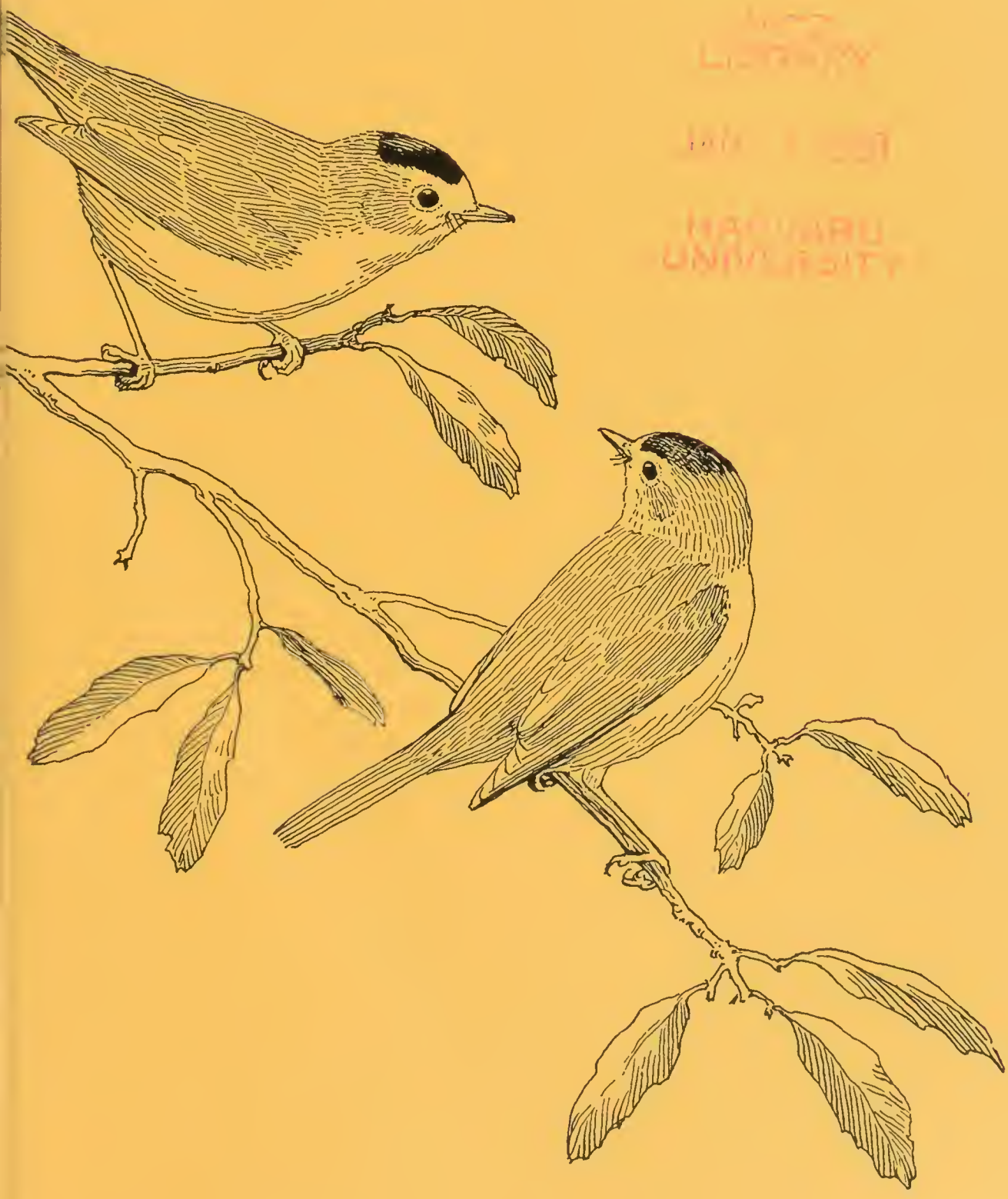

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DISPLAY BEHAVIOR, FORAGING ECOLOGY, AND SYSTEMATICS OF THE GOLDEN-WINGED MANAKIN (*MASIUS CHRYSOPTERUS*)

RICHARD O. PRUM[1] AND ANN E. JOHNSON[2]

ABSTRACT.—The displays and foraging behavior of the Golden-winged Manakin (*Masius chrysopterus*: Pipridae) were observed at two sites in western Ecuador from May to July 1985. *Masius* foraged both solitarily and with multispecies foraging flocks, and fed on fruits of 10 plant species from four botanical families. Male *Masius* occupied 30–40-m diameter display territories arranged in dispersed leks. Males defended territories through frequent advertisement calling, and performed displays on fallen logs and exposed buttress roots within each territory. Courtship display elements included a complex log-approach display, a chin-down display, and a side-to-side bowing display. Pairs of males performed coordinated log-approach and side-to-side bowing displays but the function of these coordinated behaviors was not determined. A phylogenetic analysis of display behaviors strongly indicates that *Masius* is the sister-group to the genus *Corapipo* and that *Ilicura* may be the sister-group to these two genera. These conclusions are partially corroborated by morphological and biochemical evidence. *Received 5 Aug. 1986, accepted 27 Feb. 1987.*

RESÚMEN.—Los comportamientos de alimentación y cortejo del saltarín ali-dorado (*Masius chrysopterus*: Pipridae) se observaron en dos lugares en Ecuador occidental en los meses de mayo a julio de 1985. Individuos de *Masius* buscaron comida solitariamente y en grupos multi-específicos, y se alimentaron en 12 especies de plantas de 4 familias. Los machos ocuparon territorios de 30–40 m de diámetro disputestos en "leks," o areas de despliegues colectivos, dispersos. Los despliegues de cortejo de los machos se ejecutaron sobre troncos caídos y contrafuertes adentro de cada territorio. El repertorio de cortejo incluyó un complejo despliegue de acercamiento al tronco, y despliegues de apuntar la barbilla hacia abajo e inclinarse de lado-a-lado. Parejas de machos ejecutaron despliegues coordinados, pero la función de estos comportamientos es desconocida. Un análisis filogenético de los despliegues de cortejo indica robustamente que *Masius* es el grupo-hermano del género *Corapipo*, y que

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The color frontispiece of a Golden-winged Manakin (*Masius chrysopterus*) male below a female at a buttress root display site is a mixed media painting by Paul K. Donahue.

el género *Ilicura* estaría emparentado más cercamente a éstos. Estas conclusiones sistemáticas están corroboradas en parte, por evidencia morfológica y bioquímica.

Many species of the Neotropical manakins (Pipridae) are known for their extreme sexual dimorphism, elaborate courtship displays, and lek breeding systems (Sick 1959, 1967; Snow 1963a). The patterns of variation in behavior, plumage, and morphology among the 51 species presently classified as manakins (Snow 1979) provide an excellent opportunity to investigate the evolution of nonresource-based, display-polygyny breeding systems, and to study the historical effects of sexual selection on behavioral and morphological diversification. As the courtship displays, breeding systems, and life histories of more manakin species are described, it will become increasingly possible to explore these various evolutionary questions comparatively across the family.

The monotypic genus *Masius* is found in mossy forest of the upper tropical and lower subtropical zones (500–2100 m) of the eastern and western slopes of the Andes from northwestern Venezuela to northern Peru (Meyer de Schauensee 1966, Snow 1979, Hilty and Brown 1986). The behavior of *Masius* is virtually unknown (Meyer de Schauensee and Phelps 1978, Hilty and Brown 1986), and its systematic relationships to other genera of manakins are enigmatic (Snow 1975).

In this paper we present the results of a field investigation of the diet, foraging behavior, and courtship display of the Golden-winged Manakin (*Masius chrysopterus*) in western Ecuador. We also present a phylogenetic analysis of the systematic relationships of *Masius* to other piprid genera based on courtship display behavior.

STUDY AREAS AND FIELD METHODS

Observations were made at two study sites in western Ecuador between 11 May and 28 July 1985. The first site was primary, mossy cloud forest at 1400–1700 m on Hacienda San Vicente, Mindo, Provincia de Pichincha (00°02′S, 78°48′W). The second site was selectively cut and second-growth mossy forest at 500–600 m near the village of El Placer, Provincia de Esmeraldas, on Km 303 of the Quito-San Lorenzo railroad, approximately 24 km WNW of Lita, Provincia de Imbabura (00°52′N, 78°28′W). Both sites were extremely moist; rain was recorded on nearly every day of observation, and direct sunlight was recorded on less than 20 days. Mindo is apparently seasonally drier than El Placer, which experiences much less seasonal change in precipitation (residents of Mindo and El Placer, pers. comm.). The mossy cloud forest at Mindo had an average canopy height of 10–15 m. The forest at El Placer had a canopy height of 20 m and was unusually cool and mossy for its altitude. Apparently, the extremely humid and cool conditions in this portion of the Pacific slope of the Andes and the position of El Placer in the first foothills above the Pacific coast make it possible for mossy forest to persist at much lower altitudes in this region than in other areas of the Andes.

We watched foraging male and female *Masius* for 50 h at Mindo from 11 May to 22 June

1985; none of these individuals was banded, but at least 2 adult males, 2 immature males, and 1 immature male or female were observed. We completed 164 h of observation of territorial males and 2 h of observation of foraging males and females at El Placer from 27 June to 28 July 1985. Seven adult males and one immature male were color banded, weighed, and measured in five days of mist-netting at El Placer from 29 June to 3 July. Vocalizations were recorded with Uher 4000 and Sony TCM 5000 tape recorders. Sonagrams were prepared with a Kay Digital Sonagraph 7800. Color 16-mm movies of the courtship displays were used to prepare the illustrations of the displays. Herbarium specimens of fruit plants eaten by *Masius* were identified and deposited at the University of Michigan Herbarium, Ann Arbor, Michigan.

PLUMAGE AND WEIGHT

Adult male *Masius* are velvety black with patches of bright golden-yellow (Spectrum Yellow, Smithe 1975) on the tail, wing linings, flight feathers, throat, and forecrown, and a patch of orange, red, or brown on the hindcrown (see Frontispiece). Primary and secondary flight feathers and the outer tail feathers are entirely yellow with thin black stripes along the leading edge of their outer vanes. These black edges often conceal the yellow wing and tail patches when the male is perched. The yellow forecrown is composed of thin, plush feathers that curve forward over the culmen and which may be erected posteriorly to produce a slight crest at the top of the head. The posterior half of the crown is composed of orange, red, or brown barbless feathers that are thickened and blunt in shape, and smooth and shiny in texture (similar to specialized feathers of *Bombycilla* and *Chlorochrysa*). The posterior portion of the crown cannot be erected. Laterally bordering the forecrown are two short black plumes that can be erected to form "horns" on either side of the head. Female *Masius* are generally olive-green in plumage with yellow-olive on the throat, belly, and wing linings (see Frontispiece). Immature male *Masius* first resemble females and then molt into adult male plumage. This transition begins with the yellow forecrown and throat patches and then proceeds patchily throughout the rest of the body. Both sexes have dark brown irises, purplish-pink legs, and pinkish-gray bills. Males at El Placer averaged 10.2 g (range = 9.0–12.5; N = 8), and a single female at El Placer weighed 13.5 g.

DIET AND FORAGING BEHAVIOR

Golden-winged Manakins fed on both insects and fruit during short hovering sally flights. Individuals were observed feeding on the fruits of 10 species of plants from four families: Boraginaceae—*Cordia* sp.; Melastomataceae—*Miconia theaezans, M.* cf. *arbicola, M.* sp.#1 (sect. Cremanion), *M.* sp.#2 (sect. Cremanion); Poaceae—*Olyra* sp.; Rubiaceae—*Ossaea* sp., *Palicourea* sp., *Psychotria* cf. *aviculoides, Sabicea* sp. (aff.

umbellata and *colombia*). The most important plants in the diet were the four species of *Miconia*. At Mindo, *Masius* spent almost all of their time foraging at small trees of *Miconia* cf. *theaezans*, which were fruiting abundantly there during the observation period; individuals were observed feeding only once at each of the other three species of food plants collected at Mindo. At El Placer, *Masius* were observed foraging at a wider variety of species of melastomes and Rubiaceae, including *Miconia* cf. *theaezans*.

When foraging, both sexes gave high, thin *tseet* notes (Fig. 1A) at a frequency of once every 1–20 min. These notes are extremely similar to many given by common *Tangara* tanagers at Mindo, but can be differentiated by the high, sharp quality of the initial portion of the descending call.

At Mindo, the male and female *Masius* spent over 75% of 50 h of observation foraging in multispecies flocks. This figure may be exaggerated because foraging *Masius* were most easily detected by the *tseet* notes which were given with increasing frequency during interactions with a multispecies flock. Foraging flocks included 5–10 species at a time of a total of 15 species, 7 of which (*) were nearly constantly present: *Eubucco bourcierii, Dendrocincla fuliginosa, Lepidocolaptes affinis, Phylidor rufus, Terenura callionota, Myioborus miniatus**, *Euphonia xanthogaster**, *Chlorochrysa phoenicotis, Tangara rufigula, T. arthus**, *T. icterocephala, T. xanthocephala**, *T. parzudakii**, *T. laboradorides**, *T. ruficervix, T. gyrola, T. nigroviridis**, *T. vassorii, Anisognathus flavinucha*, and *Piranga leucoptera*. During the observation period, the multispecies flocks foraged almost exclusively at *Miconia* cf. *theaezans* trees and a few other large melastomes over 6 m high. Multispecies flocks traveled at a rate of 100 m/h or more and had home ranges of at least 300 m in diameter. One to three individual *Masius* were observed in a single foraging flock at a time; a single adult male was nearly always present and immature males-females were the least frequent. Adult male *Masius* often aggressively chased female-plumaged and immature male *Masius*, excluding them from specific feeding perches or trees, and perhaps resulting in their lower frequencies of attendance at flocks. *Masius* sometimes dropped out of these flocks to continue foraging at a particular tree, or to preen. Adult males at Mindo rarely gave advertisement calls (see below), and they did not exhibit any nonresource territoriality indicative of lek behavior.

Although less time was spent observing foraging individuals at El Placer (2 h), it appeared that *Masius* at this locality did not associate with multispecies flocks frequently. In over 10 h of observation of multispecies flocks at El Placer, *Masius* was only occasionally in attendance. More typically, they foraged singly or in groups of two or three at a variety of heights from 2 to 20 m. Territorial males had several small fruit sources within their territories, which they fed on occasionally throughout the

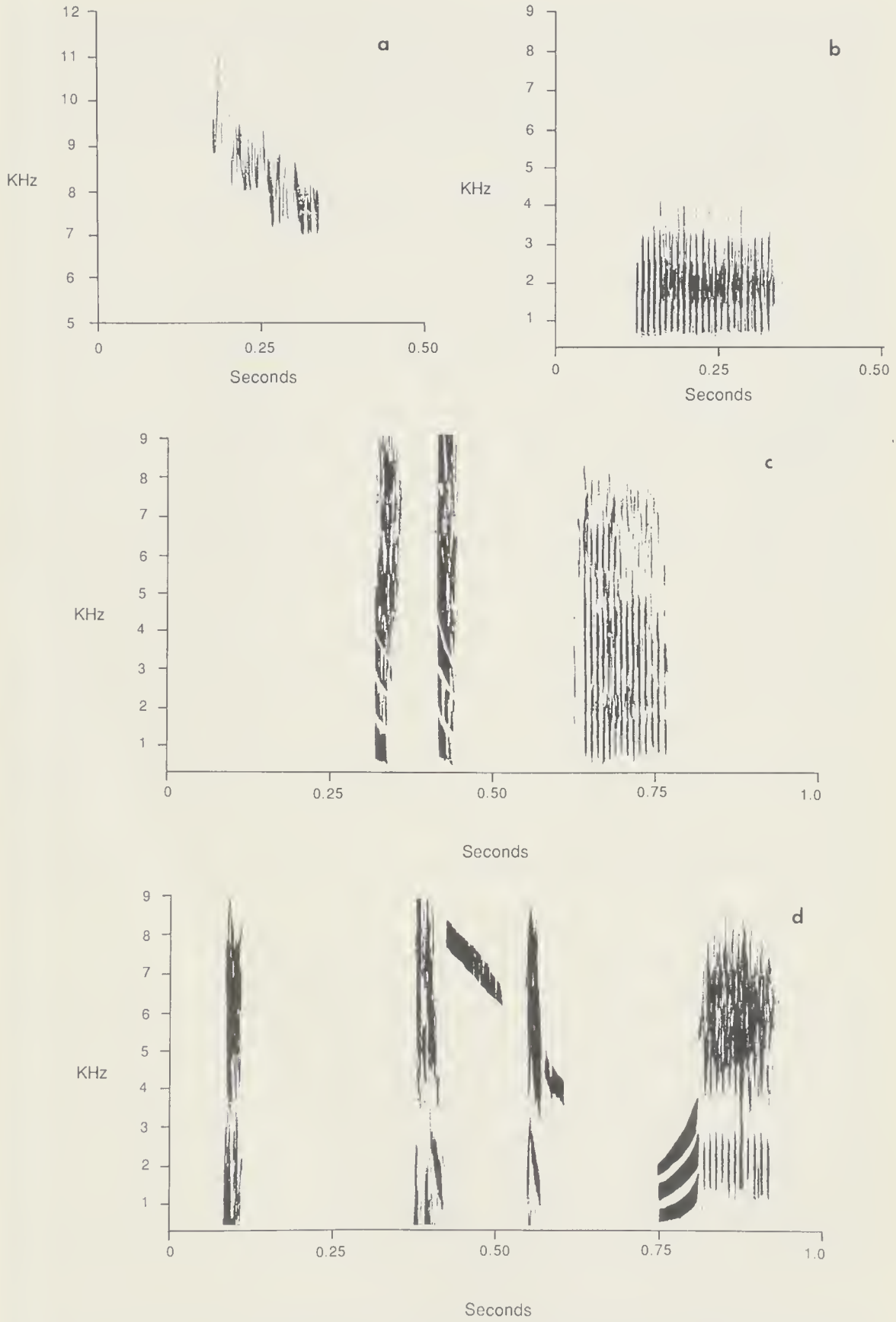

FIG. 1. Sonagrams of vocalizations of *Masius chrysopterus*: (A) foraging call, *tseet*; (B) advertisement call, *nurrt*; (C) display call, *tseet-tseet-nurrt*; (D) display call of *Corapipo gutturalis*, *pop-tickee-yeah* (see Prum 1986).

day. At particularly large fruit sources, individual *Masius* were sometimes observed in the same tree with as many as eight other bird species, including the Club-winged Manakin (*Machaeropterus deliciosus*) and the Green Manakin (*Chloropipo holochlora*). These groups, however, rarely traveled among fruiting trees in coherent associations.

SPATIAL DISTRIBUTION OF MALE TERRITORIES AND DISPLAY SITES

Male *Masius* defended territories between 25–40 m in diameter with frequent advertisement calling (see below). At the main observation site, three males maintained adjacent territories that were in auditory range of each other. This group of males was separated by 150 and 300 m, respectively, from the two nearest, other groups, which were each composed of two or more males. The male observed most extensively (W/W) sang over an area of about 25 × 40 m, but spent over 90% of its calling time within 10 m of the main display log. W/W was in attendance on his territory in over 90% of 5-min observation periods (47 h) over 15 days. In 35 h of observation of two other territorial males (G/G, and unbanded), territorial attendance was much less consistent and averaged less than 50%.

Each male territory included 2–4 fallen-log or exposed buttress-root display sites. Nine display logs and roots were located. They varied from 15 to 100 cm in diameter and 0.5 to 10 m in length and were generally free from obstructing vegetation. W/W displayed at four different logs; two of these logs were 5 m apart and formed the center of his territory, and the two other logs were 10 and 15 m away from the first two. G/G displayed at an exposed buttress root and a log that were 40 m apart at the extreme ends of his calling territory. The closest display logs of W/W and G/G were about 15 m apart.

ELEMENTS OF THE COURTSHIP DISPLAY

Advertisement calling.—The male advertisement call was a low, nasal, frog-like *harrnt* or *nurrt* (Hilty and Brown 1986) (Fig. 1B). Occasionally, the *nurrt* and *tseet* calls were combined into a single, continuous *tseet-nurrt*. Males called from many 2–4 m high perches throughout their territories, sometimes returning habitually to call from specific perches. While calling, males perched with their body plumage fluffed and with heads pulled in, concealing their yellow throat patches. When a male uttered a *nurrt* note, its head popped up briefly exposing the throat patch.

Advertisement calling began in the morning between 07:30 and 08:30 h and continued throughout the day until 18:00 h. The duration and consistency of calling varied greatly among males. In 14 h of continuous

5-min observation periods over 2 days, W/W called at an average rate of 3.2 calls/min. From the time morning activity began until the end of the series of observation periods, W/W called 1579 times in 8 h 10 min (07:50–16:00 h) on the first day, and 1053 calls in 5 h 50 min (07:55–13:45 h) on the second day. There was no consistent variation in calling frequency with the time of day, although hard rains curtailed calling whenever they occurred. The maximum calling frequency recorded in any 5-min observation period was 9.6 calls/min by W/W during a bout of counter singing with neighboring G/G. Other males besides W/W called at similar frequencies when in attendance at their territories, but they did not call as consistently throughout the day.

Log-approach display and display call.—Male *Masius* performed an aerial and vocal display when they approached their fallen-log or buttress-root display sites. For the aerial portion of the display, males flew to the display log from a perch 1–5 m high and 1–10 m from the display log, landed on the display log, immediately rebounded up into the air, and landed 30–40 cm down the log (Fig. 2a). During this rebound, males turned around in flight, exposing their yellow wing patches, which are often obscured in normal flight, and landed facing back in the direction from which they first approached the log. The log-approach display was often given silently (N = 45), but in the majority of cases males uttered a highly synchronized display call during the log-approach display (N = 90). The display call began as a high, thin, continuous, descending *seee* note which lasted from 1 to 3 sec and was given while in flight from a perch to the display log. Immediately before landing on the log, males gave a double *tseet-tseet* note that was followed immediately by a single, growling *nurrt* during the rebound flight down the log. The entire display call was performed very rapidly producing a continuous *seee . . . ee-tseet-tseet-nurrt* (Fig. 1C). In the sonograms of the display call, the introductory *seee* note appears as a thin band approximately 1 Khz wide which descends from 9 Khz to 7 Khz (not illustrated). The *tseet-tseet* notes are each composed of a number of descending parallel harmonic bands. The final *nurrt* note is composed of a series of 12–18 extremely short notes with harmonics from 0.5–7 Khz which form a single syllable about 0.015 sec long. The display call *nurrt* is very similar to the advertisement *nurrt* in structure (Fig. 1B, C). Log-approach displays were performed throughout the day from 07:30 h until 15:00 h with slightly increased frequency between 08:30 h and 10:00 h. Log-approach displays which were accompanied by display calls were much more commonly observed, but this result could be an artifact of the additional auditory cues for the observers.

Log displays.—The main courtship displays of *Masius* were performed

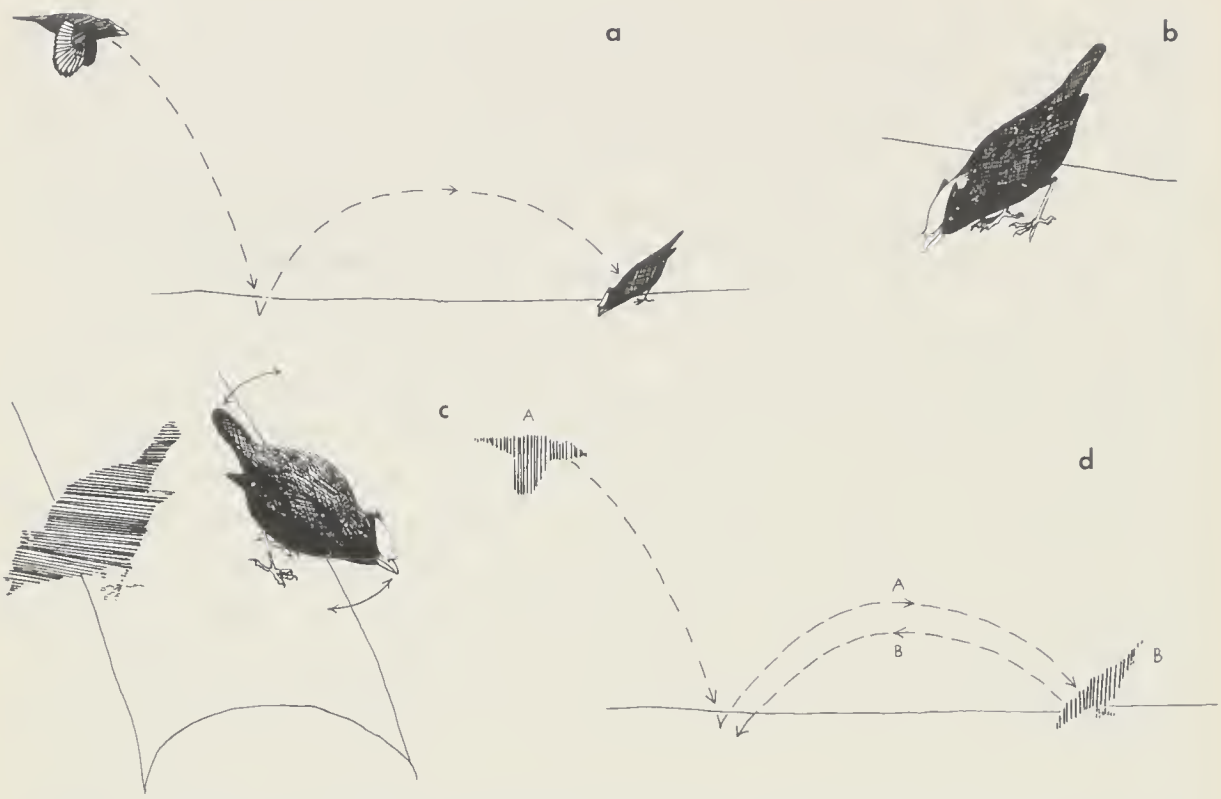

FIG. 2. Displays of *Masius chrysopterus*: (A) Log-approach display and display call. A male flies down to the log, giving a high, thin descending *seee* note (left). He then lands on the log and rebounds up, giving the *tseet-tseet-nurrt* portion of the display call (arrows at center). While rebounding off the log, the male turns in flight and lands facing back in the opposite direction (right). (B) The chin-down display. (C) The side-to-side bowing display. A male perches on a display log with his plumage fluffed out, tail cocked, and horns raised, and bows rhythmically from side to side, nearly touching his bill to the log. In between bows, a male (right) may turn 90° to 180° in place or make several short steps before making the next bow (left). (D) Coordinated log-approach display. See text for description.

on mossy fallen logs and exposed buttress roots (see Frontispiece). Once perched on the display log, males performed several distinct display elements.

Chin-down display.—While performing the chin-down display, males remained motionless with their bills nearly touching the log and their tails pointing upward at a steep angle between 60 and 90° (Fig. 2B). The body plumage was sleek in appearance, and the feathers of the yellow forecrown and black horns were erected. Males maintained this posture motionlessly for 1 to 20 sec. The chin-down display was most often performed immediately following log approaches.

Side-to-side bowing display.—Males performed an elaborate "mechanical" display in which the posterior forecrown feathers and "horns" were erected, the body plumage was fluffed out, and the tail held cocked at an angle. In this posture, males bowed rhythmically from left to right, raising

their tails, lowering their heads, and nearly touching their bills to the log (Fig. 2C). Between bows, males either turned 90–180° in place or made a few quick steps in the direction of the next bow. Each successive bow was separated by 0.5 to 1 sec. Males oriented along the long axis of the log, bowing toward either side, or facing one side of the log and bowing toward either end. Males performed this display for 30–60 sec without interruption. The side-to-side bowing display was always performed silently. This display was given during periods of increased calling and display activity, such as following repeated log approaches and display calls, and during intraspecific interactions (see below).

Stamping.—On several occasions males that were perched on display logs stamped their feet very rapidly for <1 sec, moving 2 or 3 cm ahead along the log. Although this display was infrequent and extremely short in duration, it appeared to have the stylized and nonfunctional qualities of a ritualized display behavior and was always performed while perched on the log in between bouts of side-to-side bowing.

Gardening.—While perched on a display log, males often pecked at moss and vegetation on the surface of the log or in the area immediately surrounding the log. "Gardening" behavior does not qualify as a display, but it is included here because it was always performed during bouts of log display.

MALE-MALE INTERACTIONS

Male advertisement calling usually increased in frequency and intensity during counter-singing with a neighboring male, and occasional bouts of aggression on territorial borders were observed. Nonresident adult and immature males sometimes called and displayed in male territories when the resident male was absent (N = 8). None of the visitors was banded. Display by visiting males included all the display elements described above, though many of the visiting immature males were obviously less adept at the displays than the adult males.

On about 20 occasions, pairs of males were seen displaying simultaneously on a territory. In two of these instances, the pairs were composed of two visiting males, either two adults or an adult and an immature. In the remaining instances, the pairs were composed of a resident male (G/G) and a visiting, unbanded immature male. Commonly, pairs of males began by counter-singing (*nurrt*s) and then proceeded to perform repeated log approaches and display calls. Once both males were perched on the log, they frequently engaged in synchronized or coordinated side-to-side bowing (N = 10). In the coordinated form of the side-to-side bowing display the males faced each other, separated by 10–20 cm, and bowed to either side at the same time. On one occasion, a pair of visiting adult

males performed synchronized side-to-side bowing while perched next to one another about 2 m high and about 4 m from a display log. W/W was never observed displaying with another male.

In five instances, G/G and an unbanded immature male performed a highly coordinated form of the log-approach display (Fig. 2D). While one male (male A) was approaching the log and giving the introductory *seee* note of the display call, the second male (male B) was perched on the log. As in a normal log-approach display, male A landed on the log 30–40 cm away from male B and then rebounded up from the log toward male B, giving the full display call. During the rebound, male B hopped along the log underneath male A, turned around in flight, and landed at the place where male A first landed, while male A came to rest at the same point where male B was originally perched. After pausing for a brief moment in this position, male B flew off and the display was repeated 10–30 sec later with the roles reversed. Often at the end of the display before male B flew off, both males perched in chin-down posture, facing each other without moving for a second or two. If male A assumed chin-down posture at the end of his approach, he often remained in that posture until male B began the introductory *seee* notes of the next display. At this time male A abandoned the chin-down posture and looked around in anticipation of the arrival of male B. The display occurred extremely rapidly and was always perfectly coordinated. The cycle was repeated between four and 10 times.

MALE-FEMALE INTERACTIONS

As females were impossible to distinguish from some immature males by plumage alone, behavioral criteria were used to identify presumptive females at the display sites. Adult and immature males always displayed or assumed some display posture, such as raising the forecrown and horn feathers, when visiting a display site. On three occasions, female-plumaged birds visited calling perches and display logs on a male territory without calling, attempting to display, or assuming any overtly male posture. In each instance the resident adult male (W/W) performed repeated log-approach displays, display calls, chin-down and side-to-side bowing displays to the presumptive female for between 1 and 5 min. In many of these log approaches, W/W landed first on one side of the perched female and rebounded over her landing on her other side. When the chin-down posture was performed W/W perched directly in front of the female and remained motionless for several seconds. During the side-to-side bowing display, he bowed to the left and to the right of the visiting female, clearly displaying his crown feathers with each bow. Sometimes he moved slowly toward the female with short steps between each bow, eventually dis-

placing her from that place on the log. All three interactions ended with both birds flying off. No copulations were observed. A female mist-netted at El Placer on 28 July had a well developed brood patch, indicating that females were nesting and actively soliciting mates during the time of the observations. The breeding season at Mindo has yet to be determined.

COMPARISONS OF DISPLAYS OF *MASIUS* TO OTHER PIPRIDAE

The courtship displays of *Masius* share striking and unique similarities with those of the genus *Corapipo*. The displays of the Central American subspecies of *Corapipo leucorrhoa* have been described briefly (Aldrich and Bole 1937, Slud 1964, Skutch 1967), but the display behavior of *Corapipo gutturalis* of the Guiana Highlands has been documented in some detail (Prum 1986). Both *Masius* and *Corapipo* perform their courtship displays on fallen logs or buttress roots in a manner which is unique among known manakins. The log-approach displays performed by *Masius* and *Corapipo* are identical in many respects. In both genera, males fly to the display log, immediately rebound off the log and land down the log, facing back toward where they first landed. Both species of *Corapipo* also perform a less rapid "moth-flight" log approach, an elaborate above-the-canopy log approach, and a flight-song display not performed by *Masius*. Both *Masius* and *Corapipo* give stereotyped and highly synchronized display calls during the rapid log-approach display. The display calls of both genera are characterized by (1) a long, thin introductory *seee* note or a series of *seee* notes which is given while in flight toward the log, (2) a double-syllabled note uttered as the male drops to the log (apparently single-syllabled in *Corapipo leucorrhoa*) (Skutch 1967), and (3) a final, squeaky or harsh, single-syllabled note given as the male rebounds back down the log. Although *Masius* do not produce any mechanical display sounds, both species of *Corapipo* produce a mechanical *pop* note immediately before dropping to the log. Recordings of the display calls of *Corapipo leucorrhoa* are not available, but sonograms of the display calls of *Masius* (*tseet-tseet-nurrt*) and *Corapipo gutturalis* (*pop-tickee-yeah*; Prum 1986) reveal some basic similarities in the structure of the two calls (Fig. 1C, D). The paired *tseet-tseet* and *tickee* notes are very similar in structure, and the final *nurrt* and *yeah* notes are nearly identical in form. (The final portion of the *yeah* note was incorrectly left out of the sonograms of the *Corapipo gutturalis* display call in Prum 1986). *Corapipo gutturalis* also has descending notes following each syllable of the *tickee* notes and a band of ascending harmonics preceding the *yeah* note, both of which are lacking in *Masius*. The *Masius* display call is slightly faster in tempo and lacks the introductory mechanical *pop* note.

The side-to-side bowing and chin-down displays of *Masius*, the wing-

shiver and hunched-posture displays of *Corapipo gutturalis,* and the general log displays of *Corapipo leucorrhoa* all involve a very specific posture in which the bill and foreparts are lowered until nearly touching the display log and the hindparts are distinctly raised. The side-to-side bowing display is unique to *Masius* whereas the wing-shiver and bill-pointing are unique to *Corapipo gutturalis.*

Some of these behavioral similarities are shared by the monotypic Pin-tailed Manakin (*Ilicura militaris*) of southeastern Brazil (Snow and Snow 1985). The chin-down postures of *Ilicura* and *Masius* appear to be virtually identical; indeed, males of both species even sleek their plumage during the display. The chin-down posture is also similar to the position assumed during the log displays of both *Corapipo* species. Although a "tail-up" posture is performed by the *Pipra aureola* species-group (Snow 1963b, Schwartz and Snow 1978, Robbins 1983), this posture differs in that the bird is oriented perpendicular or oblique to a thin (ca 5 mm) perch, with its head sometimes below the level of the perch. The chin-down postures of *Ilicura, Masius,* and *Corapipo* are all performed while oriented parallel to a log or large perch so that the head nearly rests on its surface.

Although generalized to-and-fro flights are a conspicuous element in the courtship displays of several known manakin species (Sick 1959, 1967; Snow 1961, 1962a; Skutch 1969; Prum 1985), there are aspects of the double *snap*-jump of *Ilicura* that this genus shares uniquely with *Masius* and *Corapipo.* Among manakins, only these three genera are known to perform a to-and-fro display in which males fly parallel to a display perch or log, turn rapidly around in midflight and land on the same perch facing directly back toward their original position. This behavioral novelty is exhibited in the log-approach displays of both *Corapipo* and *Masius,* the to-and-fro log display of *Corapipo gutturalis* and the double *snap*-jump of *Ilicura.* All of these displays are performed over the backs of females that visit display sites, implying a similarity in behavioral context as well as in the general appearance of the displays. Male *Chiroxiphia* perform a "cart-wheel" display which also entails jumping along a horizontal perch (Snow 1963b, Foster 1981), but this display lacks the abrupt turn-around in flight and the stereotyped form which characterize the displays of the other three genera.

PHYLOGENETIC ANALYSIS OF DISPLAYS OF *MASIUS* AND OTHER PIPRIDAE

Sick (1959, 1967), Snow (1963a, 1975), and others have recognized phylogenetic patterns in the courtship displays of manakins; however, attempts to formulate explicit systematic conclusions from the behavioral

similarities have been limited both by the lack of sufficient behavioral data and the problem of establishing behavioral homologies between piprid genera. Behavioral homology and the use of behavior in systematics have been discussed in detail (e.g., Atz 1970), and behavioral characters, particularly song, have been widely used in avian systematics (e.g., Payne 1986).

In order to use behavioral similarities as systematic characters it is necessary to distinguish shared derived behavioral novelties or synapomorphies, which imply exclusive common ancestry, from primitive similarities or plesiomorphies, which are not phylogenetically informative. Synapomorphies may be identified by comparing the variety of character states found in the monophyletic group in question (the in-group) to those found in its most closely-related sister-group (the out-group); by out-group comparison, those states unique to some portion of the in-group are hypothesized as derived (Eldridge and Cracraft 1980, Stevens 1980, Wiley 1981). A phylogeny may be constructed by hierarchically arranging these derived character states.

The position of *Masius* within the piprids has been enigmatic (Snow 1975). In an investigation of tyrannoid allozymes, S. M. Lanyon (1985) found that a monophyletic group containing the piprid genera *Masius, Corapipo, Chiroxiphia,* and *Chloropipo* was supported by a variety of distance and cladistic analyses, but that the relationships among these genera could not be consistently resolved. The sister-group to this clade was comprised of *Pipra, Manacus, Tyranneutes,* and *Neopelma* (Lanyon 1985). Using the former as an in-group and the latter as an out-group, it is possible to polarize the behavioral similarities described above and produce a behavioral phylogeny of the genera *Masius, Corapipo,* and *Chiroxiphia.* The genus *Ilicura* was not included in Lanyon's analysis (1985) but is included in this in-group on the basis of the behavioral characters alone. The genus *Chloropipo* is not included in this analysis because its courtship behaviors have not been described. The behavioral characters used are motor patterns which are part of courtship display and not the social contexts of these behaviors (Table 1).

The results of this analysis strongly indicate that *Corapipo* and *Masius* are sister-groups and further suggest that *Ilicura* is the sister-group to these two genera (Fig. 3). The placement of *Masius* and *Corapipo* as sister-groups is corroborated by striking similarities in their syringeal structure. Ames (1971) found that *Corapipo* was unique among all passerines examined in the structure of both its syringeal musculature and cartilages. He subsequently observed the syrinx of *Masius* and found it to be nearly identical to *Corapipo* (P. L. Ames, pers. comm.). Ames (1971) reported that the syringes of *Chiroxiphia* and *Ilicura* were distinct from the other

TABLE 1

BEHAVIORAL CHARACTERS USED IN PHYLOGENETIC ANALYSIS OF *MASIUS CHRYSOPTERUS* AND RELATED PIPRIDAE[a]

Derived behavioral characters	*Chiroxiphia*	*Ilicura militaris*	*Masius chrysopterus*	*Corapipo gutturalis*	*Corapipo leucorrhoa*
1. Cart-wheel display	1	0	0	0	0
2. Rebound from display perch or log with turn-around in flight	0	1	1	1	1
3. Display postures with foreparts lowered to perch or log	0	1	1	1	1
4. Double *snap*-jump display	0	1	0	0	0
5. Display on fallen logs or buttress roots	0	0	1	1	1
6. Log-approach display with synchronized display call	0	0	1	1	1
7. Side-to-side bowing display	0	0	1	0	0
8. Flight-song display	0	0	0	1	1
9. Butterfly log-approach display	0	0	0	1	1
10. Mechanical *pop* in log approach display call	0	0	0	1	1
11. Wing-shiver and to-and-fro displays	0	0	0	1	0
12. Throat patch erected into ruff during display	0	0	0	0	1

[a] 0 indicates absence and 1 indicates presence of derived character state. All derived character states were absent in the out-group. See text for details. References: Out-group.—Davis 1949; Prum 1985; Robbins 1983; Schwartz and Snow 1978; Skutch 1969; Snow 1961, 1962a, b, 1963a, b. *Chiroxiphia.*—Foster 1977, 1981; Snow 1963c. *Ilicura.*—Snow and Snow 1985. *Corapipo gutturalis.*—Prum 1986. *Corapipo leucorrhoa.*—Aldrich and Bole 1937, Skutch 1967, Slud 1964.

piprids examined, however the variation in syringeal structure in the family is so great that these differences cannot be considered as evidence against a close relationship among these genera. The placement of *Ilicura* in this group should be considered as a preliminary systematic prediction based on behavioral characters that should be tested by further morphological and biochemical investigation.

DISCUSSION

The composition of the diet of *Masius* is similar in many respects to those of some other manakins (Snow 1962a, b; Worthington 1982). As in many other piprids, melastomes of the genus *Miconia* are the most important plant food sources in the diet of *Masius,* followed closely by rubiaceous trees and shrubs. Our observations are too limited to conclude whether the differences in foraging behavior at the two sites were due to

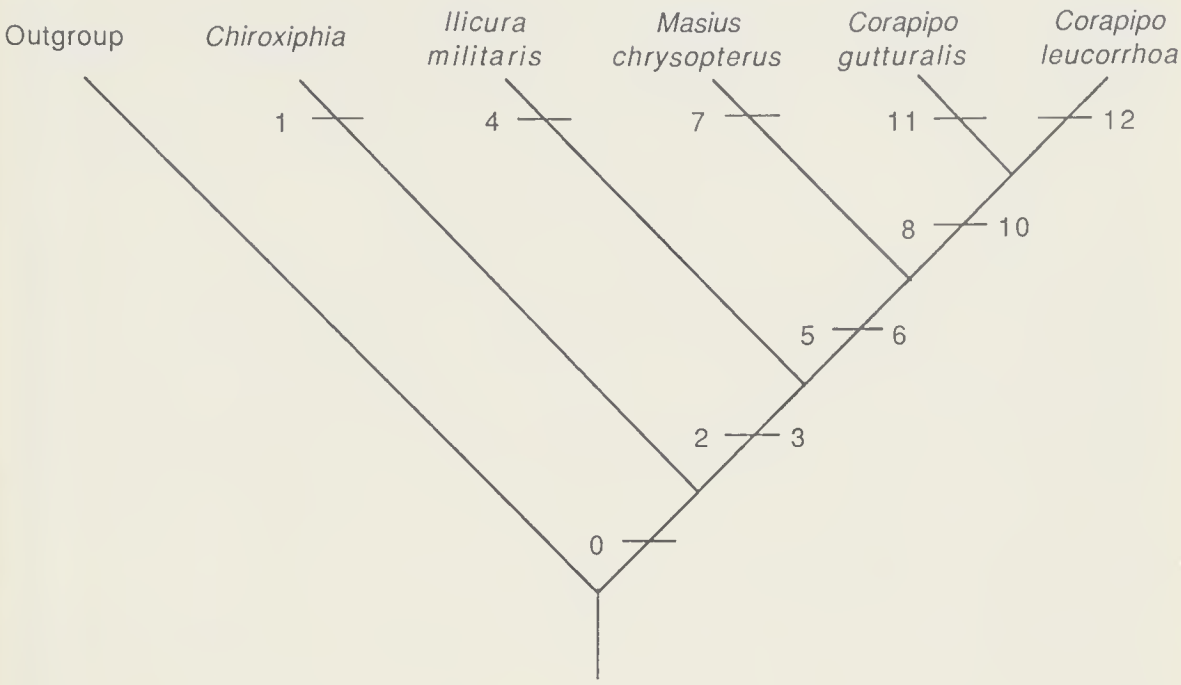

FIG. 3. A phylogeny of *Masius* and related manakins based on derived behavioral characters. Monophyly of the group *Masius, Corapipo,* and *Chiroxiphia* is based on (0) derived biochemical characters (Lanyon 1985); biochemical character states of *Ilicura* are unknown. The out-group includes *Pipra, Manacus, Tyranneutes,* and *Neopelma* (Lanyon 1985). The polarity and distributions of the behavioral characters (1–12) are detailed in Table 1. See text for description of methods.

seasonal variations in fruit availability or breeding season, or to differences in multispecies flock composition.

Masius appears to maintain display territories in dispersed leks in a manner similar to the *Pipra aureola* species-group (Snow 1963b; Schwartz and Snow 1978; Robbins 1983, 1986), the *Pipra serena* species-group (Skutch 1969, Prum 1985), *Pipra pipra* (Snow 1961), and *Ilicura militaris* (Snow and Snow 1985). Male *Masius* also perform coordinated displays with one another. Unlike Foster (1985), we define coordinated male displays as cooperative only if these behavioral patterns assist in the attraction of mates for one of the males; if a coordinated display does not serve to attract mates (e.g., ritualized aggressive behavior), it does not enhance the fitness of one male through the investment of another, and the behavior cannot be viewed as "cooperative." Given limited observations, it is not possible to identify the function of coordinated display in *Masius.* The individual variation in frequency of the behavior and the observations of female-visits in the absence of coordinated display indicate that the coordinated behavior of *Masius* is not obligately cooperative as in

Chiroxiphia (Snow 1963c; Foster 1977, 1981), and may not serve in the cooperative attraction of females at all. The male that was most consistently in attendance on his territory and that received all three observed female visits was never observed displaying with another individual. In the composition of intermale partnerships, the coordinated behavior of *Masius* appears to be most similar to the nonobligate cooperative displays of the *Pipra aureola* species-group (Snow 1963b; Schwartz and Snow 1978; Robbins 1983, 1986), but the behavior of *Masius* also appears less frequent and consistent than the coordinated displays of these species. In the *Pipra aureola* species-group, the subordinate male of a partnership has the opportunity of deposing the alpha male or inheriting the alpha male's territory (Robbins 1983, 1986). Further observations are required to determine whether this is a plausible mechanism for the maintenance of coordinated display behavior in *Masius*.

The congruence between the phylogenetic analysis of courtship displays presented above, derived biochemical characters (Lanyon 1985), and morphological evidence from the structure of the syrinx (Ames 1971, pers. comm.) strongly supports the systematic conclusion that *Masius* and *Corapipo* are sister-groups. Confidence in this sister-group relationship permits us to investigate explicitly various aspects of the divergence between the two genera. For instance, certain vocal elements common to both genera have undergone a transference of function; the *Masius* advertisement call is clearly similar to the final note of the display call, whereas *Corapipo*'s advertisement call is an elaboration of the introductory *seee* notes of the display call (Prum 1986).

Although many elements of the courtship displays of these two genera have been conserved since common ancestry, their male plumages have diverged considerably. The conservation of these behavioral traits could be due to fixation of genetic factors determining behavior. Alternatively, the difference in the rate of divergence of behavioral and morphological traits may suggest that females in this lineage have been choosing mates on the basis of variation in morphological plumage traits rather than behavioral characteristics. If female mate preferences are acting on variation in heritable male traits, then these male traits should evolve faster than others (Fisher 1958; Lande 1980, 1981; Payne 1983; West-Eberhard 1983). The divergence in male plumage could also be the result of natural selection for premating isolation mechanisms. Such selection would result in reproductive character displacement which is restricted to or accentuated in zones of sympatry, while sexual selection would produce differentiation without any geographical correlation (Payne 1983). *Masius* and *Corapipo* are sympatric in parts of all three ranges of the Colombian Andes (Hilty and Brown 1986), but male character divergence is neither

restricted to nor accentuated in these zones of contact. Thus, the hypothesis that sexual selection has produced male plumage divergence in this group is corroborated, though the mechanism for the conservation of courtship behaviors remains to be elucidated.

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COLOR PLATE

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THE MIGRATION OF SHOREBIRDS IN THE BAY OF FUNDY

PETER W. HICKLIN[1]

ABSTRACT.—Large populations of 34 species of shorebirds migrate in late summer and fall to the wide muddy intertidal areas of the upper Bay of Fundy in preparation for the transoceanic flight to South American wintering grounds. Southward migration through Fundy extends from 1 July to 11 November, although the main passage usually occurs between 20 July and 20 September. Shorebirds are most numerous during August. The average length of stay for the Semipalmated Sandpiper (*Calidris pusilla*) is 15 days. Estimates of total numbers for the migratory period of the nine most common species range between 800,000 and 1,400,000 birds. The Semipalmated Sandpiper constitutes 95% of all shorebirds recorded. The populations of Semipalmated Sandpipers stopping in the Bay of Fundy during southward migration each year represent 42–74% of the world population of this species. The Black-bellied Plover (*Pluvialis squatarola*) is the only species that migrates via the Bay of Fundy in spring in numbers comparable to those recorded in late summer and fall. *Received 16 Oct. 1986, accepted 30 Apr. 1987.*

In late summer and autumn each year, shorebirds migrate from arctic and subarctic breeding grounds to coastal staging areas in southeastern Canada and northeastern United States, where they deposit stores of fat in preparation for a nonstop flight over the Atlantic Ocean to Central and South American wintering areas (McNeil and Burton 1977, Williams et al. 1977, Morrison 1984). McNeil and Cadieux (1972:590) showed that seven shorebird species accumulated sufficient fat reserves on the Magdalen Islands in the Gulf of St. Lawrence to depart "south from Nova Scotia and the New England states on fall migration to the Lesser Antilles and northern South America." These investigators were likely unaware at that time that the Bay of Fundy proper (shared by New Brunswick and Nova Scotia) may have been the main stopover site of these birds prior to an overseas migration to South America. Large-scale movements of migratory shorebirds to the Bay of Fundy in autumn were clearly established by Richardson's (1979) radar studies in the Maritime Provinces. These studies also revealed that shorebirds left the Bay of Fundy in a southeasterly direction over the Atlantic Ocean, reaffirming McNeil and Cadieux's (1972) conclusion that the birds flew nonstop over the ocean to their wintering grounds in South America. Williams et al. (1977:257) substantiated the extensive use of an overseas migratory route by simultaneous observations of shorebird flocks from radar installations along

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the North American coast, on Bermuda, in the Caribbean, and ships at sea, during the autumn migration. By correcting for the effects of the strong easterly trade winds in the vicinity of the Sargasso Sea, they concluded that "birds could accomplish the crossing of the ocean by maintaining a constant southeast flight direction from the time they left the North American coast until they reached South America."

The return journey to the northern breeding grounds does not include a similar overseas route northward to the Bay of Fundy from the wintering area. McNeil and Burton (1977:167) indicated that most North American shorebird species departing northward from northeastern Venezuela in spring have insufficient energy reserves to fly much farther than across the Caribbean Sea, and that the spring migrants must reach their northern breeding grounds "by flying either along the Atlantic or through the Mississippi flyway." Based on morphometric studies and published accounts of shorebird numbers in spring, Harrington and Morrison (1979:96) concluded that "Semipalmated Sandpipers in eastern Canadian arctic regions apparently migrate north by an Atlantic route on the United States seaboard, probably turning cross-country in the northeastern United States and southeastern Canada." I show in this paper that there is actually very little movement of migrant shorebirds in the Bay of Fundy in spring except for Black-bellied Plovers (scientific names in Table 1). The cross-country turning point alluded to by Harrington and Morrison (1979) appears to be primarily in Delaware Bay, New Jersey, where over one million shorebirds gather in spring, including about 250,000 Semipalmated Sandpipers, to feed on the eggs of horseshoe crabs (Myers 1986). This elliptical migratory pattern, with the southward passage in autumn lying eastward of the northward route in spring, would explain why few shorebirds are recorded in the Bay of Fundy in spring, but attain large numbers in late summer and autumn. The most recent and detailed summary maps of the presumed spring and fall migratory routes of North American shorebirds can be found in Morrison (1984) and Myers et al. (1987).

Although it has long been known that the upper reaches of the Bay of Fundy harbor many shorebirds during autumn migration (Tufts 1917), published accounts regarding their numbers and the timing of migration are qualitative (Tufts 1973, Squires 1976). Morrison and Harrington (1979) presented data on maximum counts of three shorebird species present at key areas between James Bay and northern South America during southward migration in 1976. The numbers shown included nearly 318,000 shorebirds (mainly Semipalmated Sandpipers) in the Bay of Fundy, or 72.4% of the total (calculated from Table 1, Morrison and Harrington 1979), data that strongly emphasize the importance of the Bay of Fundy

TABLE 1
SPECIES OF MIGRANT SHOREBIRDS IN THE BAY OF FUNDY

Species	Relative abundance	Principal habitat
Semipalmated Plover (*Charadrius semipalmatus*)	B; U (Sp), A (Au)[a]	Mud and sand flats, salt marshes
Piping Plover (*C. melodus*)	B; R (Sp, Au)	Sand dunes and beaches
Killdeer (*C. vociferus*)	B; C (Sp, Au)	Open fields, salt marshes
Lesser Golden-Plover (*Pluvialis dominica*)	R (Sp), C–A (Au)	Mown hayfields and pastures
Black-bellied Plover (*P. squatarola*)	A–VA (Sp, Au)	Mud and sand flats, beaches, salt marshes
Ruddy Turnstone (*Arenaria interpres*)	R (Sp), C (Au)	Rocky and sandy beaches
Common Snipe (*Capella gallinago*)	B; C–A (Sp, Au)	Salt and freshwater marshes, pastures, mown hayfields
Whimbrel (*Numenius phaeopus*)	R (Sp), U–C (Au)	Beaches, blueberry fields
Spotted Sandpiper (*Actitis macularia*)	B; C (Sp, Au)	Beaches, salt and freshwater marshes
Upland Sandpiper (*Bartramia longicauda*)	U (Sp, Au)	Upland pastures and fields
Solitary Sandpiper (*Tringa solitaria*)	R (Sp, Au)	Freshwater ponds
Greater Yellowlegs (*T. melanoleuca*)	U (Sp), A (Au)	Salt marshes, mudflats, occasionally beaches
Lesser Yellowlegs (*T. flavipes*)	U (Sp), A (Au)	Salt marshes, mudflats, occasionally beaches
Willet (*Catoptrophorus semipalmatus*)	B; U (Sp, Au)	Salt marshes, occasionally mudflats
Red Knot (*Calidris canuta*)	R (Sp), C–A (Au)	Salt marshes and mudflats
Purple Sandpiper (*C. maritima*)	O; R (Sp, Au)	Rocky intertidal
Pectoral Sandpiper (*C. melanotus*)	R (Sp), U–C (Au)	Salt marshes
White-rumped Sandpiper (*C. fuscicollis*)	R (Sp), C–A (Au)	Beaches, mudflats, and salt marshes
Baird's Sandpiper (*C. bairdii*)	R (Sp), U (Au)	Beaches, mudflats, probably salt marshes
Least Sandpiper (*C. minutilla*)	U–A (Sp), A (Au)	Beaches, mudflats, salt marshes

TABLE 1
CONTINUED

Species	Relative abundance	Principal habitat
Curlew Sandpiper (*C. ferruginea*)	R (Sp, Au)	Beaches and mudflats
Dunlin (*C. alpina*)	R (Sp), C–VA (Au)	Beaches and mudflats
Semipalmated Sandpiper (*C. pusilla*)	C–A (Sp), VA (Au)	Beaches, mudflats, and salt marshes
Western Sandpiper (*C. mauri*)	R (Sp, Au)	Beaches, mudflats, and salt marshes
Sanderling (*C. alba*)	R (Sp), A (Au)	Beaches and mudflats, probably salt marshes
Short-billed Dowitcher (*Limnodromus griseus*)	R (Sp), A (Au)	Beaches, mudflats, and salt marshes
Long-billed Curlew (*L. scolopaceus*)	R (Sp, Au)	Salt marshes, probably mudflats
Stilt Sandpiper (*C. himantopus*)	R (Sp, Au)	Beaches and salt marshes
Marbled Godwit (*Limosa fedoa*)	R (Sp, Au)	Beaches and salt marshes
Hudsonian Godwit (*L. haemastica*)	R (Sp), U–C (Au)	Beaches, mudflats, and salt marshes
American Avocet (*Recurvirostra americana*)	R (Sp, Au)	Salt marshes
Red Phalarope (*Phalaropus fulicaria*)	C–A (Sp), VA (Au)	Pelagic
Wilson's Phalarope (*P. tricolor*)	R–U (Sp, Au)	Freshwater marshes
Red-necked Phalarope (*P. lobatus*)	A (Sp), VA (Au)	Pelagic

[a] B = breeding, O = overwintering, Sp = Spring, Au = Autumn, R (rare) = 5 individuals and not seen every year, U (uncommon) = 10 and seen every year, C (common) = 10–100, A (abundant) = 100–1000; VA (very abundant) = >1000.

as a shorebird staging area along the eastern seaboard during southward migration.

Population estimates based on annual maximum counts, however, presumably represent only a portion of the total number of migrants which pass through a staging area such as the Bay of Fundy over a 6- to 8-week migratory period. No attempt has been made previously to describe the timing of migration of the most numerous species and to estimate the total populations of shorebirds migrating through the Bay of Fundy during the late summer and fall.

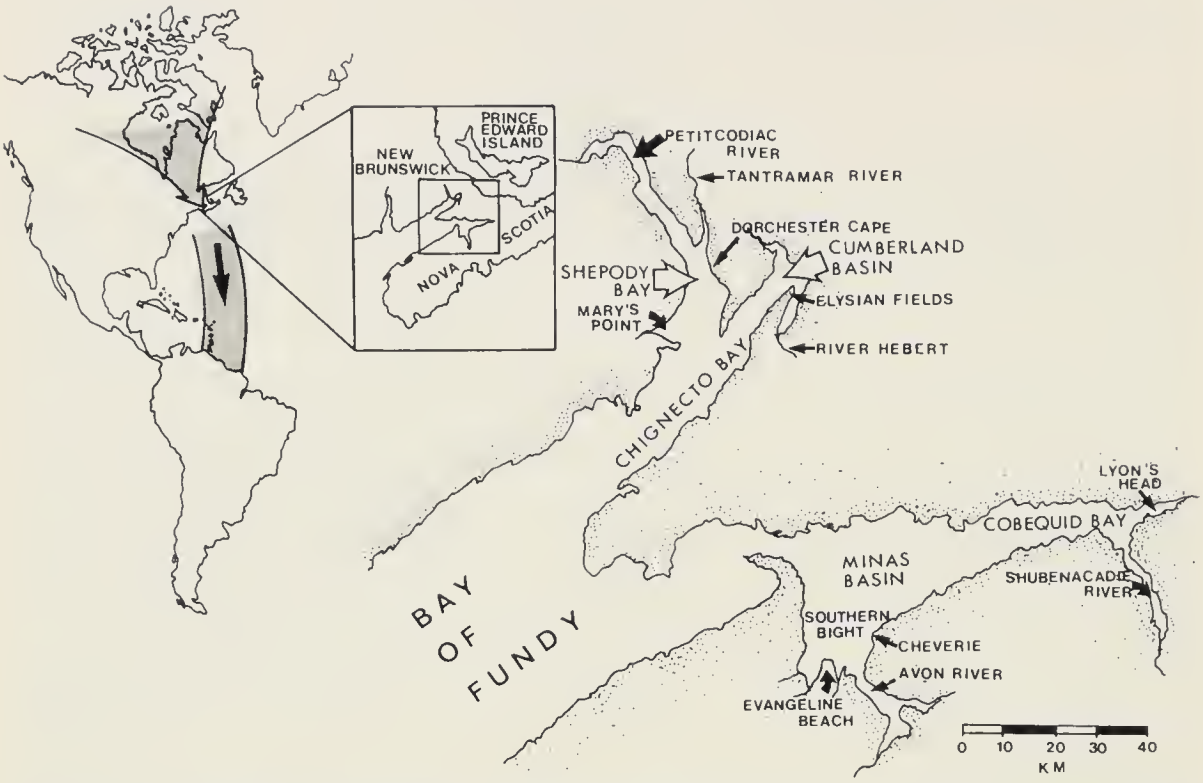


FIG. 1. The Bay of Fundy and its location along the autumn shorebird migratory flyway over the Atlantic Ocean to overwintering grounds in South America.

Thirty-four species of migrant shorebirds have been recorded in the Bay of Fundy during southward migration (Table 1). In this paper, I present information regarding the abundance, distribution, and migratory timing of the nine most common species that migrate annually to the Bay of Fundy and, typically, forage on intertidal mud and sand flats at low tide and roost on open beaches during high tide periods. These are the Black-bellied Plover, Semipalmated Plover, Short-billed Dowitcher, Red Knot, Sanderling, Least Sandpiper, Semipalmated Sandpiper, and White-rumped Sandpiper. I also included the Hudsonian Godwit which, although uncommon in the Bay of Fundy, was easily identifiable. Excluded are several other species that occupy principally fresh and salt water marshes, are rare, or occupy specialized habitats inland. Phalaropes, although numerous in autumn at the mouth of the Bay of Fundy, are not included here as these were the focus of a separate study (R. G. B. Brown, pers. comm.).

THE BAY OF FUNDY

The Bay of Fundy forms a natural boundary between the provinces of New Brunswick and Nova Scotia. The upper reaches of the bay bifurcate into two main embayments: (1) the Minas Basin and Cobequid Bay cutting eastward into Nova Scotia, and (2) Chignecto Bay pointing north into New Brunswick. Chignecto Bay further divides into Shepody Bay to the north and Cumberland Basin to the northeast (Fig. 1).

Some of the highest tidal amplitudes anywhere in the world have been measured in these areas. Tidal maxima of 17 m occur in Cobequid Bay. At mean low water, about 5000 ha of salt marsh and 35,000 ha of mud and sand flats are exposed (Pearce and Smith 1974).

The muddy intertidal zone supports a high-density, low-diversity assemblage of largely deposit-feeding invertebrates of which the burrowing amphipod *Corophium volutator* is a dominant component both numerically and by biomass (Yeo and Risk 1979, Hicklin et al. 1980). This amphipod, and to a lesser extent marine polychaetes, and the bivalve *Macoma balthica,* constitute the main prey of migrant shorebirds during autumn migration (Hicklin and Smith 1979, 1984; Gratto et al. 1984; Peer et al. 1986).

METHODS

The numbers of birds encountered at roost sites in Fundy are very large. Because of this and the wide distances between roosting areas and the relatively rapid passage of birds, I was unable to rely on a single comprehensive method of estimating total numbers stopping in the bay each year over a study period of eight years. The methods I describe here served to provide data on estimates of (1) total populations; (2) numbers of adults from air and ground surveys, respectively, conducted in 1976; (3) numbers of adults and immatures at the peak of the migratory period averaged over all survey years; and (4) ranges in population size of each species, and all species combined, using a turnover rate of 15 days as determined from color-marking studies (see below).

The count data for these estimates were obtained from aerial surveys in 1976 and from ground counts conducted by myself and volunteer observers between 1975 and 1983. In 1981, I banded and color marked Semipalmated Sandpipers to obtain some measure of turnover rate that could be applied to the ground-count data and thus account for birds which presumably had arrived and departed between censuses.

The analysis and interpretation of the data has required four important assumptions: (1) aerial and ground estimates by the same or different observers were comparable and provided a reasonably accurate reflection of absolute numbers, (2) movements of birds between roosts were minimal, (3) the rate of turnover was the same between years and roosting sites, and (4) the same rate of turnover was applicable to all species. There is some evidence to support assumptions 1 and 2, and this is presented in the appropriate sections that follow. I have no evidence to support or deny assumptions 3 and 4: data on turnover rate were obtained for one species only (Semipalmated Sandpiper, by far the most numerous), at a single site (Dorchester Cape), and for one year only. I treat the different survey methods and calculations of population size separately below.

Aerial surveys.—Between 19 July and 14 September 1976, I made 10 aerial surveys of the shorelines of Minas Basin, Cobequid Bay, and Chignecto Bay during high tide periods to locate shorebird roosting sites and to estimate the numbers of birds present. Surveys were conducted using a Cessna 172 high-wing airplane flying 25–50 m above the coastline at an average speed of 150 km/h. Most shorebird roosts encountered could be seen and numbers estimated before, or as, the birds flushed. I regularly ground-checked roosts in the Southern Bight, Minas Basin, the day before and the day following an aerial survey. Ground observers were also present at selected locations during each flight so that species identifications and counts could be compared. All counts were undertaken while birds were roosting.

Ground censuses: large roosts.—Ground censuses were undertaken regularly at three main roosting areas: (1) Evangeline Beach in the Southern Bight, Minas Basin, (2) Dorchester Cape, and (3) Mary's Point in Shepody Bay (Fig. 1). Counts of shorebirds on Evangeline Beach were made almost daily during high-tide periods from spring to late fall, 1975 and 1976 (Elliot 1977, Hicklin 1981). Additional counts of Semipalmated Plovers at Evangeline Beach were made in 1980 (Peach 1981). Similarly, volunteer observers censused shorebirds

daily in July, August, and September at Dorchester Cape and Mary's Point in 1976–1983 and 1976–1981, respectively. Less regular counts were made from April to June and October to November at all three locations.

Throughout the surveys, immature birds were identified by plumage whenever possible. However, separating the numbers of immatures from those of adults, especially for the numerous calidrine sandpipers, was often difficult and unreliable. I determined the ratio of adults to birds-of-the-year by comparing secondary peaks (identified as comprising mainly immature birds) with the earlier adult peaks at Evangeline Beach, Dorchester Cape, and Mary's Point, for each year between 1976 and 1983.

The same four observers, including myself, were responsible for taking counts at those three sites throughout all the years of this study. Two methods of counting were used, most often by two observers together or, on occasion, independently on the same day. One method involved doing a "head count" at a roost early in the migration period (18–25 July) until the day it contained about 1000 birds. Once this figure was reached, numbers increased rapidly and it became impossible to take exact counts from that time on. The observer would then count a portion of a flock, 500 or 1000 birds, and multiply this number by an appropriate order of magnitude which represented the entire roost. For example, I would count X birds in a portion of a roost then estimate that there were twice, three times . . . or 10-times as many birds in the remainder of the flock. A second method relied on data on the densities of roosting sandpipers obtained from overhead photographs of a large roost taken at Dorchester Cape in 1977. The photos were taken with a 600-mm Novaflex telephoto lens from the roof of a summer cottage. The pictures were enlarged and the birds inside three 10.5-m^2 sections of the roost, measured in the field and marked on the photographs, were counted. The densities inside the squares were 55, 65, and 68 birds/m^2. A rectangle representing 31.5 m^2 of the same roost contained 1986 birds for a density of 63 shorebirds/m^2. As the roosts in Fundy typically take on a square or rectangular shape, not unlike a large feathered carpet on the beach, an observer in the field could note markers along the edges of a roost (e.g., large stones, driftwood, seaweed) and, once the birds left the site to feed, measure by pacing the distances between the markers. The calculated area of the roost in m^2 was then multiplied by 60 to provide an estimate of the numbers of roosting birds. Often, the results obtained by the two observers on the same day using both methods were similar (e.g., $\pm$ 10,000 birds for roosts estimated at around 100,000). The two estimates were averaged except for occasions when only one estimate was available. These means of estimating numbers applied principally to flocks of Semipalmated Sandpipers, with Least Sandpipers and Semipalmated Plovers often mixed in. The large shorebirds such as Black-bellied Plover, dowitcher, knot, and Hudsonian Godwit were much less numerous and could often be counted individually.

Miscellaneous sites.—Outside of the three main roosting areas, I counted birds at irregular intervals in small bays, creeks, and salt marshes (hereafter referred to as miscellaneous sites) in the upper Bay of Fundy between 1975 and 1983. I also extracted data for the Bay of Fundy (mainly southwestern New Brunswick and Minas Basin) for miscellaneous sites from the results of the Maritimes Shorebird Survey Scheme (MSSS, ground surveys conducted by volunteers in 1974–1981), organized and coordinated by the Canadian Wildlife Service (see Morrison and Campbell 1983 for an example of the annual report series produced between 1976 and 1983). Because of the relatively small numbers of birds in those areas, they could be counted accurately.

Banding: estimating length of stay.—I present some results of the color-marking procedures here as they are relevant to the section that immediately follows. More detail on the derivation of turnover rate is also given in the Results section. In 1981, I determined the length of stay of Semipalmated Sandpipers based on observations of 1216 color-marked birds. I

attempted to catch birds daily at Dorchester Cape using mist nets at high tide, in daytime, between 20 July and 26 August. Sandpipers were captured on 29 banding days for an average daily catch of 43 ± 33 birds. Each bird was color-marked with a nontoxic fluorescent spray paint in a manner which identified the 5-day period in which a bird was initially captured. Each day, prior to banding, the numbers and color combinations of marked sandpipers in the roost were recorded. Fourteen percent of the 702 marked sandpipers subsequently seen following capture were also found at Mary's Point, Hopewell Cape, and Minudie (see Fig. 1). These areas were checked regularly, though not on a daily basis, and data from marked birds seen at these sites are included in turnover rate calculations. As I could not recognize individual birds to calculate an average length of stay (a more desirable method), I chose the median date between the day the largest proportion of birds marked on 20–30 July was recorded (30 July) the day when the lowest proportion of that sample was present (9 August) as an average date of departure (see Fig. 4B). The period between the first day of capture (also the first day the migrants arrived at the site) and the median date, gave an average length of stay of 15 days. Admittedly, this is a crude means of estimating length of stay, but under the conditions where many tens of thousands of birds roost in tightly packed flocks and feed over very wide intertidal areas (about 15 km^2 at Dorchester Cape alone), encountering a large sample of the same individuals over many days is extremely difficult. (In 1982 we placed numbered leg flags on 1795 sandpipers but failed to find a sufficient number of individuals, from which the numbers on the leg flags could be read, to obtain any meaningful data.) I therefore used this value of 15 days, as determined from the 1981 sample, as the turnover time.

In the Species Accounts that follow I use the terms "peak number" to signify the single highest count recorded at any one location in a particular year and "maximum number" to signify those counts that represent 50% or more of the peak number for each location and year.

Calculations of population size.—(a) Aerial surveys.—I totalled the numbers of all species groups for each flight. The numbers of birds were recorded from the air as "peeps" (Semipalmated Sandpiper, Least Sandpiper, Sanderling, Semipalmated Plover, and Spotted Sandpiper. Medium-sized shorebirds (Black-bellied Plover, Short-billed Dowitcher, Ruddy Turnstone, and knot) and large shorebirds (Hudsonian Godwit, yellowlegs, and Willet). I summed these totals for all species groups combined to give an overall estimate of all the birds encountered from the air for the period 19 July–14 September. The primary objective of the aerial surveys was to determine the relative abundance and distribution of shorebirds over the entire upper Bay of Fundy shoreline, many parts of which were otherwise inaccessible by any other means. Although the population estimate obtained from aerial surveys is less accurate than those based on ground surveys, I nonetheless include it here since this technique provides the most complete coverage and some means of comparison with the ground census results.

(b) Ground surveys.—In 1976, volunteers and I were able to survey a large number of roost sites in the bay than in any subsequent year. Some previously unknown roosting areas, identified from the air that year, were ground-censused one or two days following a flight. Because of their relative inaccessibility, some of these sites were occasionally surveyed after 1976 but not in all years. For these reasons, I treat the 1976 estimates separately. Moreover, the ground census data in 1976 are presented independently of the aerial surveys.

Using the ground census data, I extracted and summed the highest single-day counts for each species in 1976 to obtain an estimate of the total number of adults (peak numbers of adults were always much larger than those of immature birds for all species) in the Bay of Fundy at the height of the migratory period.

The adult peak numbers described above provide estimates for one year only. Unfortu-

TABLE 2

NUMBERS OF ARRIVALS AND DEPARTURES OF ADULT SEMIPALMATED SANDPIPERS AT EVANGELINE BEACH 1976 AND CALCULATION OF THE RATIO, ESTIMATE/PEAK NUMBER[a]

Peak numbers per 5-day period		Arrivals and departures based on a 15-day stopover		
Period	Numbers at roost site	Arrive	Stay	Depart
30 June–4 July	521	521	0	0
5–9 July	252	0	252	269
10–14 July	10,000	9748	252	0
15–19 July	10,000	0	9748	252
20–24 July	20,000	10,252	9478	0
25–29 July	30,000	19,748	10,252	9748
30 July–3 August	40,000	10,000	19,748 + 10,252	0
4–8 August	40,000	10,252	10,000 + 19,748	10,252
9–13 August	12,000	0	10,252 + (10,000 − 8252[b])	19,748 + 8252[b]
14–18 August	6000	0	(10,252 − 4252)	1748 + 4252
19–23 August	6000	6000	0	6000
24–28 August	6000	0	6000	0
29 August–2 September	0	0	6000	0
3–7 September	0	0	0	6000
Totals		66,521		66,521

[a] Calculation: Peak number for season = 40,000. Ratio: $\frac{\text{Estimate}}{\text{Peak number}} = \frac{66,521}{40,000} = 1.66$.

[b] The highest counts between 4–8 August and 9–13 August dropped by 28,000; therefore, of the 10,000 that arrived on 30 July–3 August, 8252 were eliminated to account for the large decline.

nately, simultaneous large-scale ground and air surveys, as were done in 1976, were not undertaken in subsequent years. I therefore computed average peak numbers (=average of highest single day counts) for each species at each of the major roosting areas, using ground census data only, for all survey years (Evangeline Beach: 1975, 1976; Mary's Point: 1976–1981; Dorchester Cape: 1976, 1979–1983). I summed the averages for all sites by species to give a general estimate of total population of adults which incorporated any variations in peak numbers between years. I computed averages rather than presenting only maximum numbers because of errors likely to be inherent in estimating such large numbers where absolute numbers are unobtainable.

I also calculated the average peak numbers of shorebirds at miscellaneous sites surveyed between 1974 and 1981. I added these to the average peak numbers computed from the data for the three main roosting sites and thus obtained totals for each species which included all censused roosting sites in the Upper Bay of Fundy over all years. In effect, these data provide information on the number of adults of each species that could be expected in the Bay of Fundy in an average year during the peak of the migratory period.

I calculated the ratio of adults to birds-of-the-year by comparing secondary peaks (iden-

TABLE 3

POPULATION ESTIMATES OF SEMIPALMATED SANDPIPERS AT THREE MAJOR ROOST SITES BETWEEN 1975 AND 1981 BASED ON 15-DAY TURNOVER RATE (SEE TABLE 2 FOR SAMPLE CALCULATION)

Location and year	Peak number	Population estimate	Estimate/ peak number
Evangeline Beach 1975	22,000	44,000	2.00
Evangeline Beach 1976	40,000	66,521	1.66
Dorchester Cape 1976	72,000	145,200	2.02
Dorchester Cape 1979	120,000	257,394	2.14
Dorchester Cape 1980	100,000	143,200	1.43
Dorchester Cape 1981	125,000	190,405	1.52
Dorchester Cape 1982	90,000	165,500	1.84
Mary's Point 1976	150,000	218,766	1.46
Mary's Point 1977	350,000	473,000	1.35
Mary's Point 1978	100,000	168,300	1.68
Mary's Point 1979	100,000	183,535	1.84
Mary's Point 1980	150,000	239,400	1.60
Mary's Point 1981	120,000	147,500	1.23

tified from ground surveys as comprising mainly immatures) with the earlier adult peaks, for each year, at Evangeline Beach, Dorchester Cape, and Mary's Point. The ratios, expressed as percentages, were averaged for each species over the years surveyed and the results multiplied by the average total number of adults (methods described above) to provide an estimate of the average number of immatures. Adding the estimates for adults and immatures resulted in an estimate of average peak numbers for both age groups for each species censused.

In separate calculations using the data for Semipalmated Sandpipers obtained from the three main roost sites, I broke down the survey data for each roost by year into identical 5-day periods. Each 5-day period between 10 July and 17 September included, on average, 36 ± 6 counts (range: 28–40, N = 13) with fewer counts in spring (1 May–29 June: 11 ± 3, range: 4–17, N = 12) and late fall (18 September–21 November: 11 ± 4; range: 4–15, N = 13). I used the highest number of birds recorded in each of these periods as the total number of birds in that roost for that segment of time. To these data I applied a 15-day rate of turnover. In other words, on day 15 of migration a roost would have consisted of early arrivals (peak number for days 1–5) plus those birds that arrived in the second (days 6–10) and third periods (days 11–15). On day 16 of migration I subtracted the number of the earliest flock (i.e., peak number for days 1–5) from the total, assuming that those birds had deposited sufficient fat for the completion of their migration and had left the area. If the numbers of birds in the subsequent period (days 16–20) had increased, I assumed that the difference consisted of new arrivals. If it decreased, I eliminated the difference as outgoing migrants, assuming that these birds arrived with fat reserves accumulated elsewhere (e.g., Gulf of St. Lawrence) (see McNeil and Cadieux 1972) and left early (i.e., they stayed in the area for less than 15 days). I then summed the total number of birds which had entered and left the area throughout the migratory period for each roost. I then compared each new total with the peak number in each roost, by year, to obtain a ratio of total to peak number. A sample calculation is shown in Table 2. Using this procedure, I obtained population estimates ranging between 1.23 and 2.14 times the single-day peak number observed each year (Table 3). For convenience, I rounded off this range to 1.25 to 2.00 times the peak number. I

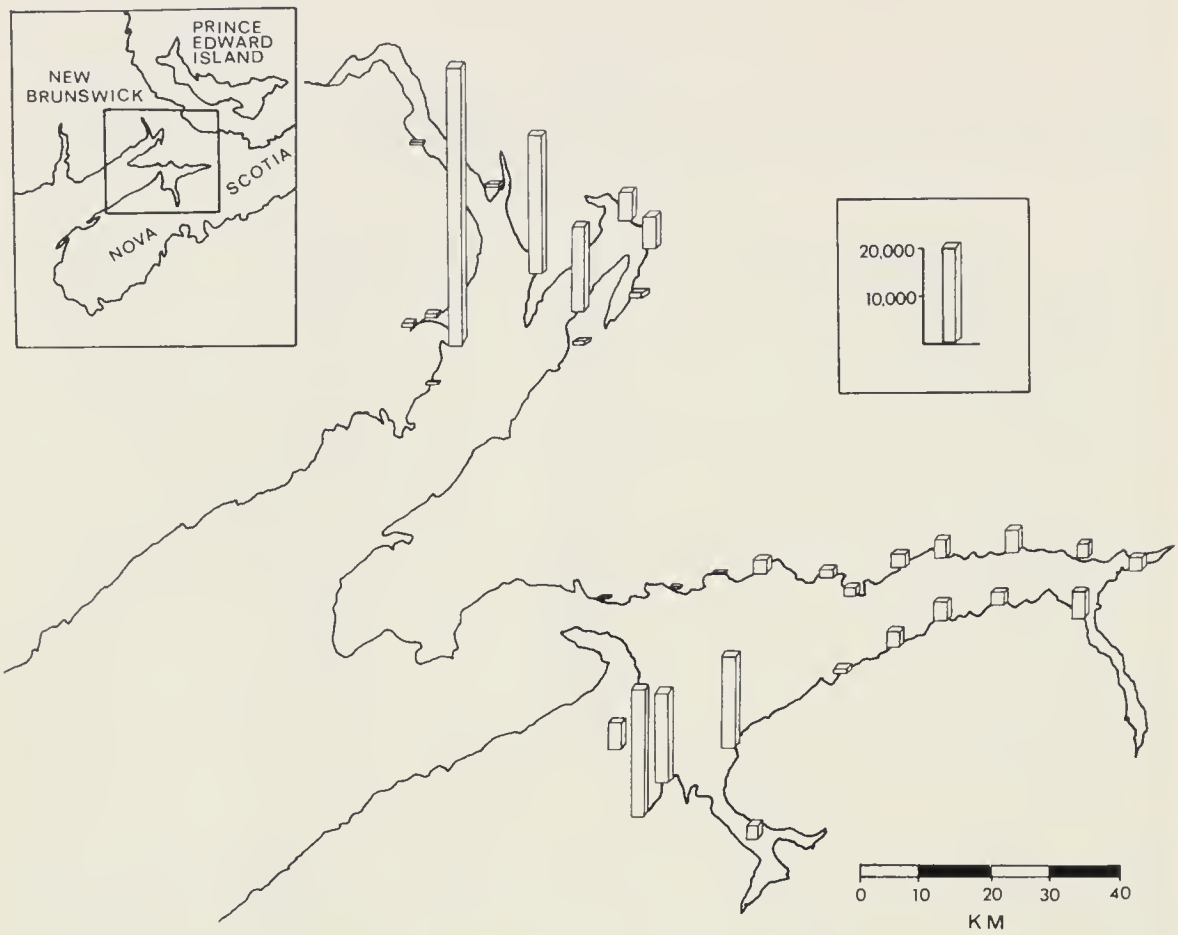


FIG. 2. Average number of shorebirds per roost based on 10 aerial surveys 19 July–12 September 1976.

therefore estimated the population of a species migrating through the upper Bay of Fundy by adding up the average peak numbers of adults and immatures for each roost site (plus miscellaneous sites) and multiplied this total by 1.25 and 2.00 to account for turnover resulting in a range within which population numbers should fall in any given year.

RESULTS

Distribution and abundance.—A total of 1,550,000 shorebirds was recorded over the 10 aerial surveys in 1976. Thirty-four roost sites were identified; the average number of shorebirds per roost throughout the July–September survey period ranged from 10 to nearly 58,000 birds for an overall average of 7000 birds per roost. The six largest roosts with 20,000 or more birds were in Shepody Bay, Cumberland Basin, and the Southern Bight, Minas Basin (Fig. 2). Numbers averaged 2600 birds per roost in other parts of Minas Basin and in Cobequid Bay. Tidal rivers such as the Petitcodiac River (Shepody Bay), River Hebert, Tantramar River (Cumberland Basin), Avon River (Southern Bight), and the Shubenacadie River (Cobequid Bay) contained comparatively low numbers (Fig. 2).

TABLE 4
PEAK NUMBERS OF SHOREBIRDS RECORDED IN 1976 FROM GROUND OBSERVATIONS

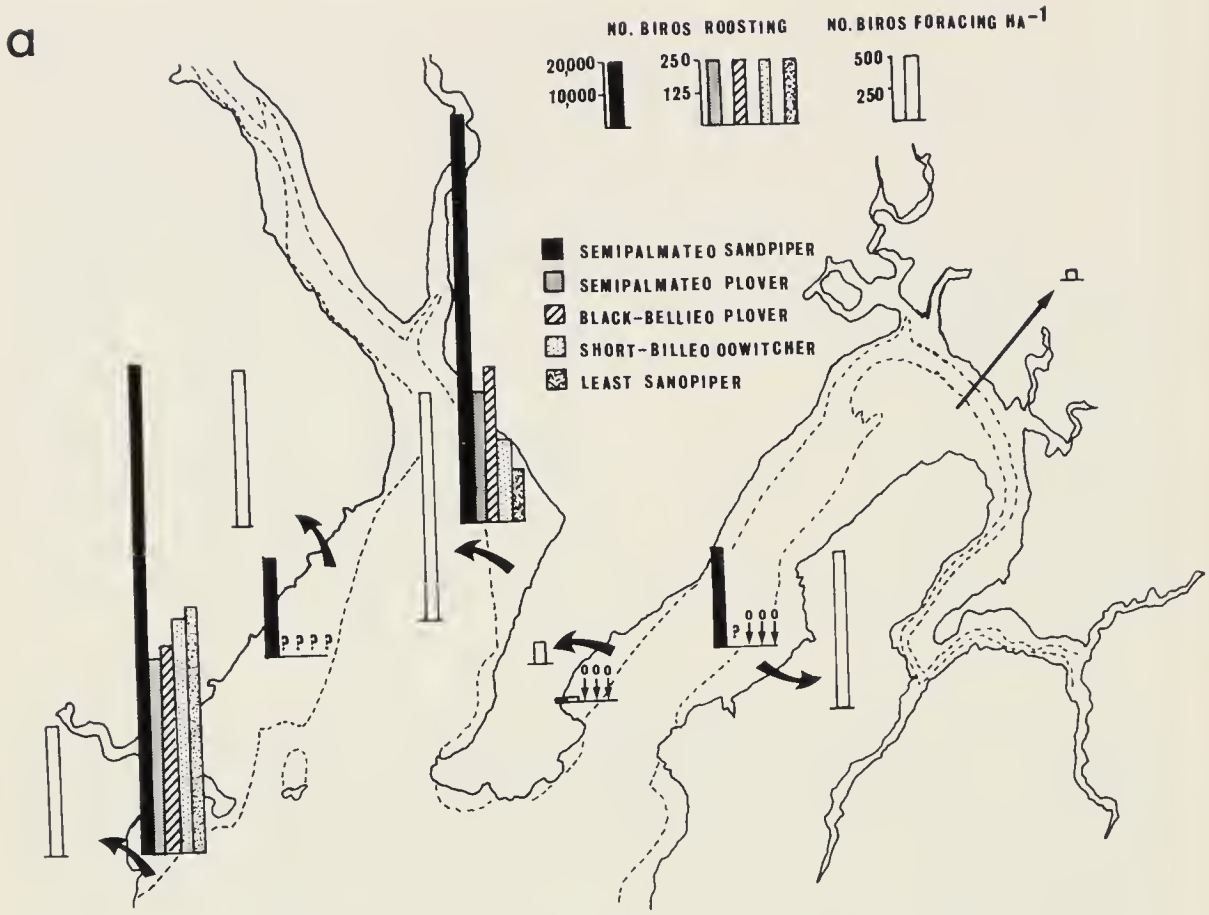
Species	Evangeline Beach	Dorchester Cape	Mary's Point	Miscel-laneous sites	Total
Black-bellied Plover	1113	345	600	1701	3759
Semipalmated Plover	122	230	600	7543	8495
Short-billed Dowitcher	886	150	900	2299	4235
Red Knot	9	75	150	132	366
Sanderling	4	100	750	1114	1968
Least Sandpiper	37	50	1000	7518	8605
Semipalmated Sandpiper	40,000	72,000	150,000	274,884	536,864
All species					564,312

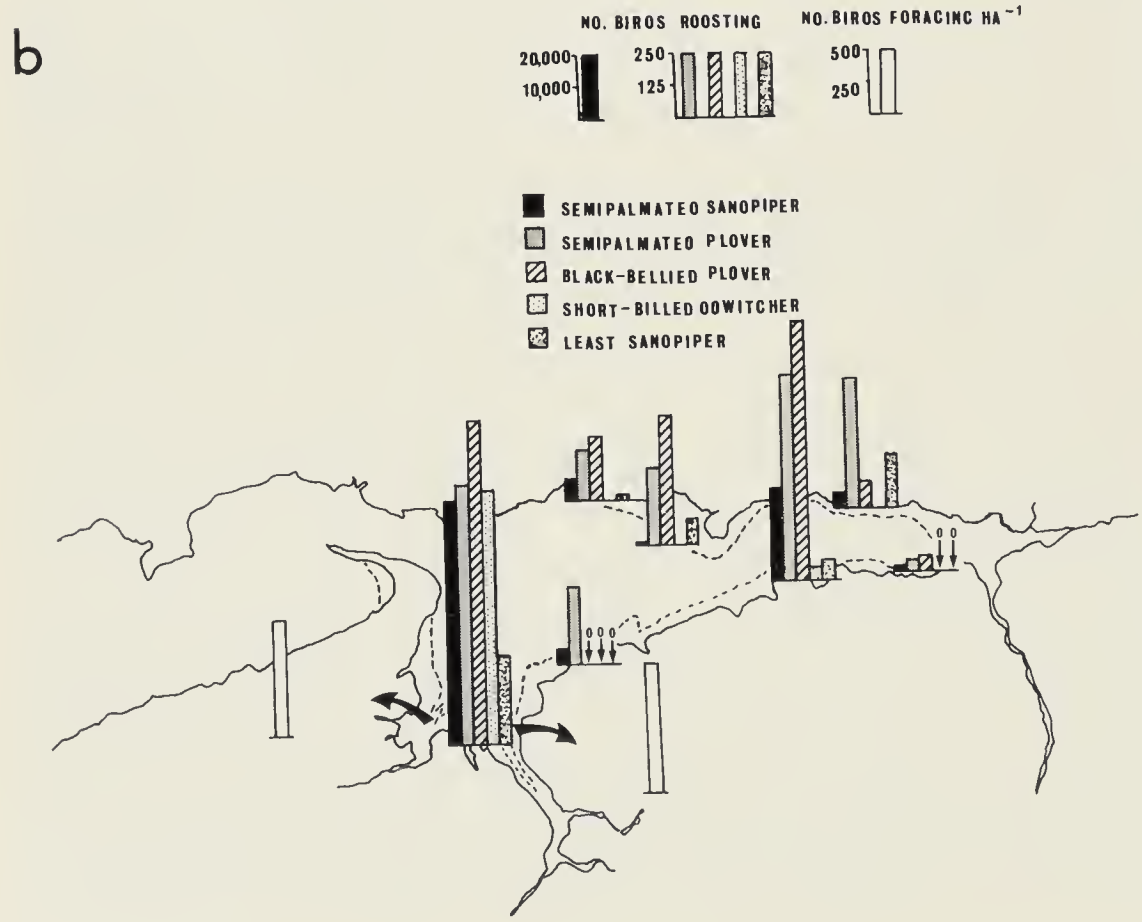
The maximum number of shorebirds recorded in one day in the upper reaches of the bay was 566,000 birds on 29 July 1976. Summation of peak numbers obtained by ground observers the same year was 564,312 (Table 4). This is a surprisingly close correspondence with the estimates made from the air. The three largest roost sites (Evangeline Beach, Dorchester Cape, and Mary's Point) accounted for 48.8% and 46.4% of those totals, respectively. The Semipalmated Sandpiper was by far the most numerous species and made up 95.1% of the total number of shorebirds recorded on ground surveys. If a 15-day turnover rate is applied (see below) to the ground survey data, then the total population migrating in Fundy in 1976 is estimated at 705,400 to 1,128,600 birds.

Ground observations made in 1976–1983 showed that the Semipalmated Sandpiper was more abundant at roost sites in Chignecto Bay than in Minas Basin and Cobequid Bay (Fig. 3A, B). Numbers of Semipalmated Plovers, Black-bellied Plovers, and Short-billed Dowitchers were high in the Southern Bight, and the two plover species were more widespread and collectively more numerous in Minas Basin and Cobequid Bay than elsewhere (Fig. 3A, B).

Some areas that had been identified as important sites based on results obtained from aerial surveys in 1976 were subsequently shown to be less important following repeated ground surveys in later years. Examples include the Elysian Fields in the Cumberland Basin and Cheverie and Lyon's Head in Cobequid Bay. Some sites such as Mary's Point, Dorchester Cape, and Evangeline Beach, however, may be termed "traditional" roosting areas because they are used by large numbers each year.

Turnover rate: Semipalmated Sandpipers.—Less than 1% of adult Semi-


a
NO. BIROS ROOSTING
NO. BIROS FORACING HA⁻¹
20,000
10,000
250
125
500
250
SEMIPALMATEO SANDPIPER
SEMIPALMATEO PLOVER
BLACK-BELLIEO PLOVER
SHORT-BILLEO OOWITCHER
LEAST SANOPIPER


b
NO. BIROS ROOSTING
NO. BIROS FORACINC HA⁻¹
20,000
10,000
250
125
500
250
SEMIPALMATEO SANOPIPER
SEMIPALMATEO PLOVER
BLACK-BELLIED PLOVER
SHORT-BILLED OOWITCHER
LEAST SANOPIPER

palmated Sandpipers color marked early in migration, 20–25 July, were seen as late as 23 August, a duration of 31 ± 3 days. The largest proportions of sandpipers marked 20–25 July and 26–30 July were recorded in the area on 30 July (13.0% and 7.9%, respectively) (Fig. 4B). Sightings of marked birds decreased quickly from 30 July onwards, indicating a rapid movement out of the area between 31 July and 9 August (Fig. 4B). Similarly, daily estimates of the numbers of sandpipers at the roost site declined after 30 July (Fig. 4A). The highest proportion of birds weighing more than 40.0 grams occurred 30 July–4 August, and there was a substantial and sudden decrease in mean fresh weights between 1 and 2 August (P. W. Hicklin, unpubl. data) which further supports these departure dates. The color-marking data indicated that there were five separate and recognizable departure periods from the Dorchester Cape site between 31 July and 20 August (Hicklin, unpubl. data). Unfortunately, I could only determine the arrival dates of those birds which left the site between 30 July–9 August (the first birds were seen on 20 July and numbers increased rapidly until 30 July, so birds arrived in that 10-day period) and not of later-arriving sandpipers. Hence, only those data are presented here. The results obtained from the color-marked sample of birds captured 20–30 July showed that a major flight out of the area began around 31 July–1 August and continued daily until 9 August.

I assume that birds that might have initially arrived with some fat reserves stayed at least 10 days, and that lean arrivals may have stayed for as long as 20 days. I therefore chose the median date of 4 August as an average date of departure for birds which first arrived as early as 20 July, regardless of the numbers present or weight. The relatively low percentages of marked birds we found in roosts were not due to any biased mortality of birds which were captured, banded, and color marked. Predation is not a factor of any significance in the Bay of Fundy during shorebird migration, and dead marked birds or their remains were never found. Rather, the difficulty of finding a few marked birds amongst large assemblages of roosting sandpipers, as are found in Fundy, is the primary reason for the relatively low percentages from which turnover was derived.

Although this estimated length of stay applied to the Semipalmated

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FIG. 3. Maximum numbers of Semipalmated Sandpipers, Semipalmated Plovers, Black-bellied Plovers, Short-billed Dowitchers, and Least Sandpipers at roosting sites and densities on foraging areas (numbers counted inside 1-ha plots on mudflats) in (a) Chignecto Bay and (b) Minas Basin and Cobequid Bay 1976–1982. Open bars (feeding densities) refer to all species combined.

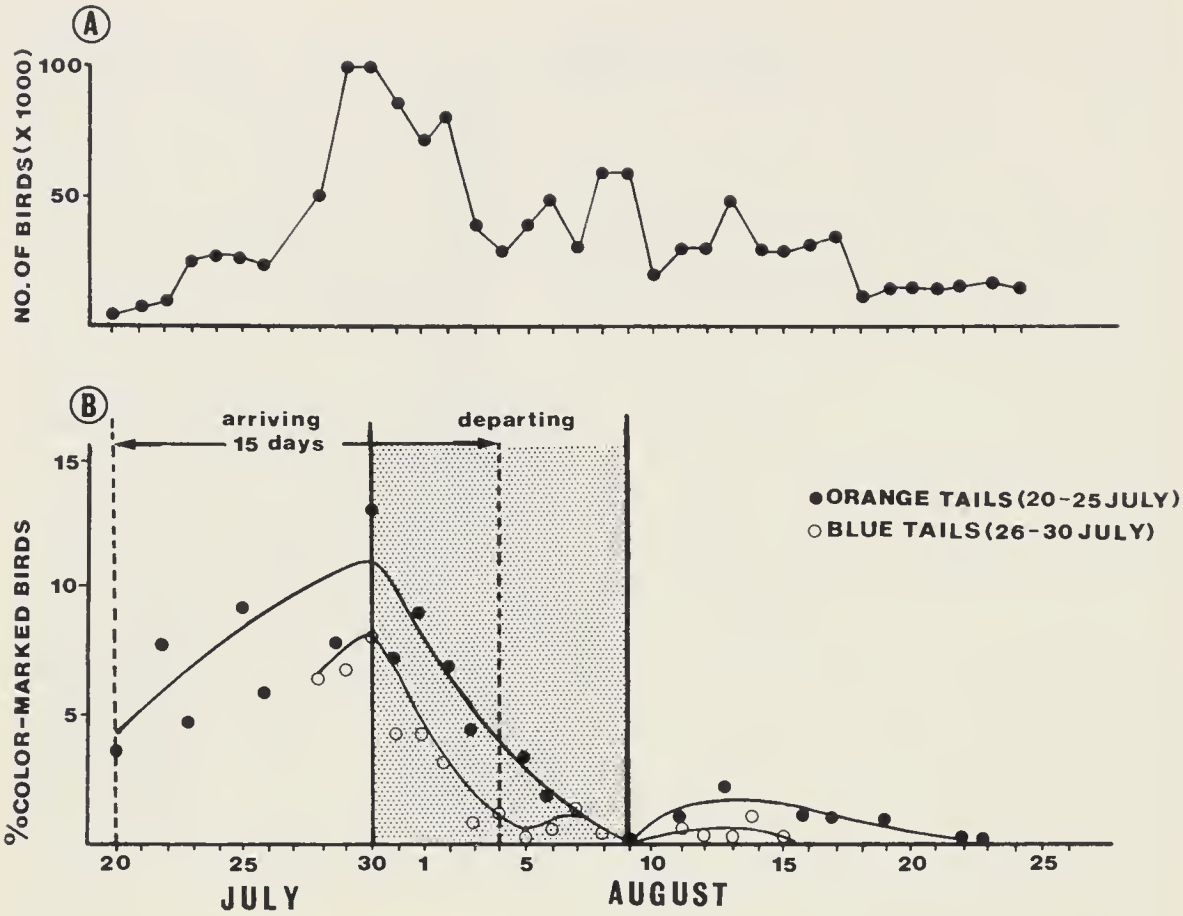

FIG. 4. A. Numbers of Semipalmated Sandpipers roosting at Dorchester Cape, 20 July–26 August, 1981. B. Daily sightings of color-marked Semipalmated Sandpipers at Dorchester Cape expressed as the percent of the total numbers of each color marked at the time of observation.

Sandpiper, I also used it to calculate the total numbers of eight other species passing through Fundy (see below). So far, it is the only means available to provide a broad estimate of numbers of these other species until further research is done. In any case, as 95% of all the birds in Fundy during autumn migration are Semipalmated Sandpipers, fluctuations in total numbers would be reflected mainly by changes in numbers of that species.

SPECIES ACCOUNTS

Black-bellied Plover.—This plover was the only species that occurred in large numbers during spring migration. The largest spring roost, at Dorchester Cape on 4 June 1983, contained 1387 birds. On average, the spring migration of Black-bellied Plovers extended from 26 April to 24 June, with peak numbers between years recorded 31 May–4 June (Fig. 5).

Southward migration in late summer began 25–29 July, and peak numbers were reached, on average, from 24 to 28 August (Fig. 5). The largest

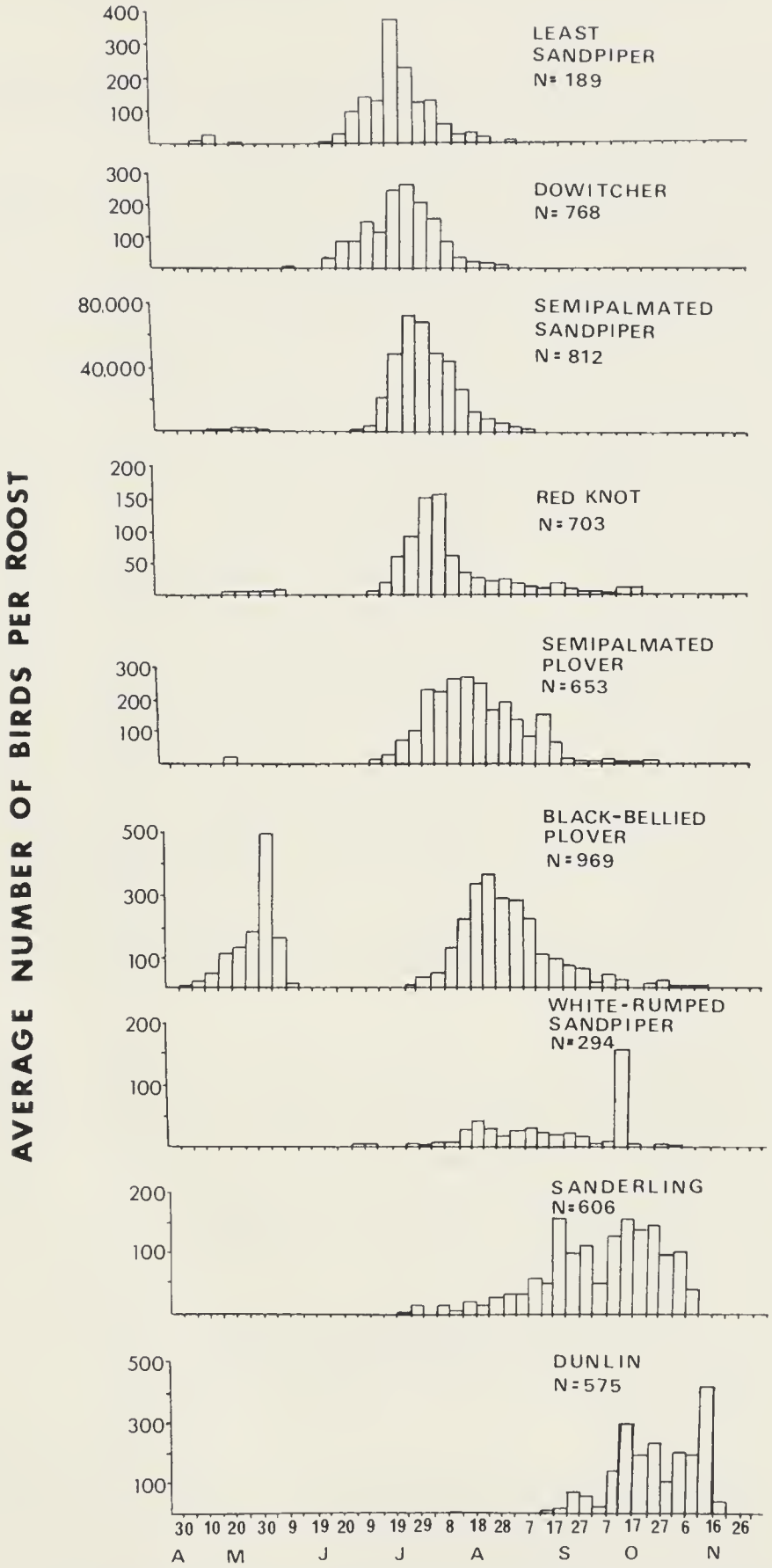

FIG. 5. Average number of shorebirds per 5-day period at Evangeline Beach, Dorchester Cape, and Mary's Point combined 1975–1983. N refers to the total number of counts for each species over all years.

roosting flock seen in late summer was of 1440 birds at Evangeline Beach on 27 August 1975.

Immatures were not seen at roost sites before 10 September. Elliot (1977) saw the first immatures at Evangeline Beach on 18 September 1975; peak numbers (300) were attained on 7 October, and the last immature bird was seen there on 11 November 1979 and at St. Andrews, New Brunswick, on the same date in 1985 (pers. obs.). On average, the peak numbers of immatures represented 20.6 ± 9.0% [SD] (N = 11) of the adult peaks. For all sites surveyed, average peak numbers of both age groups totalled 5050 birds (Table 5). Accounting for turnover, I estimate the total number of Black-bellied Plovers passing through the Bay each fall to be from 6300 to 10,000 birds (Table 5).

Semipalmated Plover.—This plover was uncommon in spring; 103 birds seen at Dorchester Cape on 23 May 1983, was the largest number recorded. In late summer and fall, Semipalmated Plovers were seen between 30 June and 6 November. Migration generally began around 15–19 July, and maximum numbers were reached on 19–23 August (Fig. 5). For all years combined, however, there was no well-defined peak, with large numbers recorded throughout the period 30 July–27 September (Fig. 5). Sites near the mouth of the Saint John River (Quaco Bay, Manawagonish Marsh, Saint's Rest Marsh and Maces Bay), Passamaquoddy Bay (Kent Island, St. Andrews), Grand Manan, and Minas Basin (Highland Village, Economy) contained large assemblages of Semipalmated Plovers, many more than were found at the three main roosting areas (Table 5, see also Appendix 1).

Although immatures were seen as early as 11 August, they did not contribute significantly to total numbers until the first week in September. The August immatures probably represented birds hatched from the southernmost part of the breeding range, in the maritimes, the Gulf of St. Lawrence, and Newfoundland (Godfrey 1966). At Mary's Point, the earliest peak of immatures occurred on 9 September 1981, and the latest at Evangeline Beach on 19 September 1975. Immature peaks averaged 19% of adult peaks at these sites. Assuming a 15-day turnover period, the population of Semipalmated Plovers passing through the Bay of Fundy is estimated to be from 13,600 to 22,000 birds (Table 5).

Short-billed Dowitcher.—Few dowitchers were recorded in spring. A flock of 100 was seen on 16 June 1979 at Mary's Point, that probably included nonbreeding birds or failed breeders. Typically, spring (between 8 May and 12 June) sightings of dowitchers consisted of flocks with fewer than five birds. In late summer and fall, dowitchers were seen 30 June–30 September. This species was the earliest southbound migrant to arrive in Fundy in substantial numbers, beginning 30 June–4 July, and peak

TABLE 5

POPULATION ESTIMATES OF SHOREBIRDS IN THE BAY OF FUNDY DURING LATE SUMMER AND FALL BASED ON MEANS OF PEAK NUMBERS 1974–1983,[a] INCLUSIVE

	Black-bellied Plover	Semi-palmated Plover	Red Knot	Sanderling	Semipalmated Sandpiper	Least Sandpiper	White-rumped Sandpiper	Dunlin	Dowitcher	Totals
Adults										
Evangeline	1278	735	0	0	31,000	346[b]	136[b]	0	968	
Dorchester Cape	484	407	300	239	118,000	346	136	1216	407	
Mary's Point	725	525	408	458	161,667	346	136	375	550	
Miscellaneous[c]	1701	7543	132	1114	273,220	7518	903	170	2299	
Total Adults	4188	9200	840	1811	583,887	8556	1311	1761	4224	598,666
% immatures	20.6	19.0	?	?	12.6	12.6[d]	?	?	24.8	
Total adults and immatures	5050	10,948	840+	1811+	657,457	9634	1311+	1761+	5271	694,093
Population estimate	6312–10,100	13,685–21,896	1050–1680	2264–3622	821,821–1,314,914	12,042–19,268	1639–2622	2201–3522	6589–10,542	867,603–1,388,166

[a] Mary's Point = 1976–1981; Dorchester Cape = 1976–1983; Miscellaneous = 1974–1981.

[b] Although the numbers of these species were not regularly identified and counted at Evangeline Beach and Dorchester Cape, the few counts available suggest that the numbers there were similar to those seen at Mary's Point.

[c] See Appendix 1.

[d] See text.

numbers were attained one month later in the period 30 July–3 August (Fig. 5). The largest single flock of 1100 birds was seen at Dorchester Cape on 27 July 1979. Comparatively few dowitchers were seen at roost sites when Semipalmated and Black-bellied plovers became abundant in late August.

No effort was made to distinguish age classes. Elliot (1977) noted that paler birds were seen after 15 August and were probably immatures. I therefore used the numbers of dowitchers seen after 15 August at the three main roost sites to estimate the proportions of immatures to adults. These amounted to 24.8% ± 9.9% (N = 14) of the adult peaks.

Outside the three main roosts, the birds were most numerous in southwestern New Brunswick (Appendix 1). Summation of counts from all areas provided an estimate of 4224 adult dowitchers at the peak of the migratory period. Including immatures and correcting for turnover, the estimated number of dowitchers passing through the Bay of Fundy is 6500 to 11,000 birds (Table 5).

Red Knot.—Knots were rarely seen in spring. Two were identified at Mary's Point on 2 June 1979, and the largest spring flock consisted of 39 birds at Dorchester Cape on 12 June 1983.

Postbreeders first appeared at these two main roost sites around 14–24 July and reached peak numbers 9–13 August (Fig. 5). In 1975 and 1976, Red Knots were seen only occasionally at Evangeline Beach, and the largest flock there consisted of 20 birds.

As peak numbers of knots recorded between 14 July and 15 August probably represented adult birds, I estimated population numbers of that age group only. The numbers of knots seen at sites other than the three main roosting areas were relatively low (Appendix 1). Based on these data, the population of adult Red Knots in Fundy is estimated to be from 1000 to 1700 birds (Table 5).

Sanderling.–Sanderlings began their migration to the Bay of Fundy in mid-July. The time of arrival of larger flocks varied among years. Maximum numbers were recorded from 13 August to 6 November, but the main movement occurred between 17 September and 6 November (Fig. 5).

In July, some of the early arrivals were in breeding plumage and may have been failed breeders or nonbreeders. From August on, all Sanderlings seen were in basic plumage, making distinction between adults and immatures very difficult. In other species where age classes could be distinguished, adults always constituted the first and largest peaks in numbers. I have therefore used early peak numbers to estimate the populations of adults only. For all sites combined (see Appendix 1), the numbers of adult Sanderlings migrating to the Bay of Fundy is estimated as 2000–3700 birds (Table 5).

Least Sandpiper.—Least Sandpipers roosted with the more numerous Semipalmated Sandpipers, and the two species were often difficult to separate. A greater effort to distinguish and count Least Sandpipers was made at Mary's Point during 1976–1981. Very few birds were seen there in spring. Maximum numbers of adult Least Sandpipers were recorded on 10 July through 13 August; maximum numbers of immatures occurred from 19 August to 17 September. On average, peak numbers of adults were reached on 25–29 July (Fig. 5).

Except for 1976 and 1979, almost twice as many immatures as adults were seen at Mary's Point. Counts of birds at other roosting or feeding areas totaled approximately 7500 birds, with large numbers concentrated in salt marshes (Appendix 1).

More effort was made to distinguish Least Sandpipers from Semipalmated Sandpipers at Mary's Point than at the other main roosting areas. Assuming that the proportions of Least to Semipalmated Sandpipers were similar at all three sites, I have therefore substituted the same average numbers as at Mary's Point for Evangeline Beach and Dorchester Cape. The number of adult Least Sandpipers in all of the Bay of Fundy is estimated at 8600 birds (Table 4). Assuming that the relative numbers of immature Least Sandpipers are similar to those of the Semipalmated Sandpiper (12.6%; see below), I estimate the population, including both age classes, as 12,000–19,000 sandpipers (Table 5).

Semipalmated Sandpiper.—The Semipalmated Sandpiper is by far the most numerous shorebird during migration in Fundy. In spring, the numbers recorded at Evangeline Beach, Dorchester Cape, and Mary's Point ranged from 428 to 10,000 birds between 21 May and 9 June. Maximum numbers at these three sites occurred in the period 20 July–23 August, and the largest roost seen was a single flock at Mary's Point containing about 350,000 sandpipers on 10 August 1977. For all years combined, peak numbers at those three sites occurred 30 July–7 August and averaged 70,000 birds per roost (Fig. 5).

The first juveniles were difficult to detect because of the large numbers of adults present. In the course of banding operations, the first immatures were captured on 14 and 19 August at Dorchester Cape in 1981 and 1982, respectively. After 23 August, the numbers of immatures captured exceeded those of adults, and from 25 August to 12 September (last banding day) nearly all the sandpipers captured were immatures. To obtain a measure of the numbers of immatures in relation to those of adults, I compared the peak numbers of sandpipers seen after 25 August with peak numbers before that date. On average, the secondary peaks amounted to $12.6 \pm 6.6\%$ ($N = 13$) of adult numbers.

Outside of the three main roosting areas, peak numbers of Semipal-

mated Sandpipers totalled about 275,000 (Appendix 1). For all sites combined, average peak numbers reached a total of nearly 584,000 sandpipers. By adding immatures and correcting for turnover, the estimated population of Semipalmated Sandpipers in the Bay of Fundy during southward migration is estimated as 800,000–1,300,000 (Table 5), which corresponds closely to the figures obtained from the air and ground surveys in 1976 (see above).

White-rumped Sandpiper.—This species was not abundant at any of the sites surveyed. At the three main roost sites, fewer than 10 were recorded in late June and early July. At Mary's Point, where the most detailed observations were made, they were not seen regularly until the middle of August. Four counts made between 13 and 17 October in 1976 and 1978 were unusually high and may reflect the passage of larger numbers of immatures during that short period in those years (Fig. 5). Similarly, White-rumped Sandpipers were scarce at other sites, except for a large flock of 600 seen at Manawagonish Marsh in 1974 (Appendix 1). If we assume that adults occurred at Evangeline Beach and Dorchester Cape in numbers similar to those counted at Mary's Point, then on average, their total numbers in the Bay of Fundy in late summer and fall lie in the range of 1600 to 3000 birds (Table 5).

Dunlin.—Dunlins are the latest migrant to pass through the bay in fall. The main passage of Dunlins occurs throughout October and early November (Fig. 5). I have no records of Dunlins from Evangeline Beach, and Tufts (1973) did not mention any notable concentrations for the area. Most birds were seen at Mary's Point and Dorchester Cape (Table 5) (Appendix 1). Based on those data, the total numbers of Dunlins migrating through Fundy is estimated as 2000 to 3500 birds (Table 5).

Hudsonian Godwit.—This large shorebird is seen each year at the main roost sites, although never in large numbers. In 1975–1983, 141 sightings of Hudsonian Godwit were recorded in Chignecto Bay for an average of 8 birds per sighting (Fig. 6). The largest single flock (80) was recorded along the Tantramar River at the head of Cumberland Basin on 29 July, 1978 (A. J. Erskine, pers. comm.). They are most commonly seen from mid-July to the latter part of August. The total number of godwits passing through Fundy in most years is probably about 100 birds.

DISCUSSION

I used three different methods: (1) aerial and (2) ground surveys in 1976 and (3) summation of the average peak numbers of adults between 1974 and 1983 to estimate the total number of adult shorebirds at the peak of the migratory period. Considering the sizes of bird flocks and the numbers of years and observers involved, there is close agreement among the three

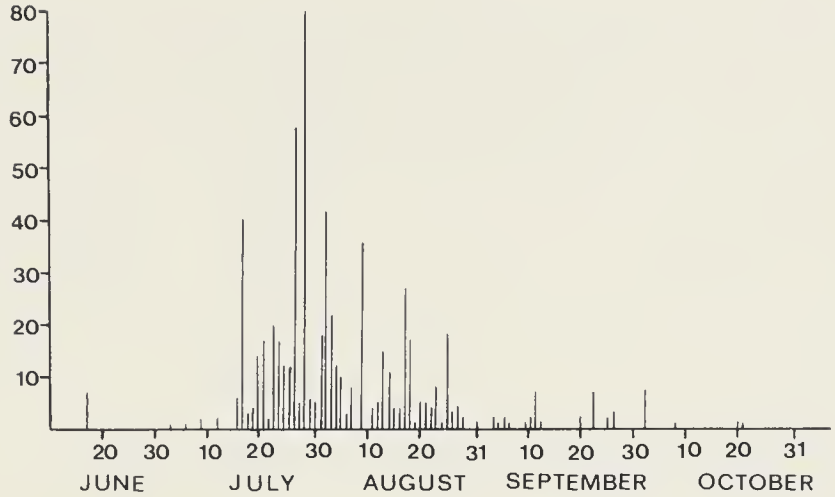

FIG. 6. Numbers of Hudsonian Godwits seen in the Bay of Fundy between 1975–1983, inclusive. Where counts were made on the same date, but in different years, the largest number was used.

estimates, which were 566,000, 564,000 and 599,000, respectively (Table 6). By adding the estimated numbers of immature birds, the total reaches slightly more than 694,000 plovers and sandpipers (Table 6).

These numbers refer only to those flocks of shorebirds recorded each year at the height of migration, and only at the sites most accessible to observers. This figure should therefore serve as a minimum estimate for the whole population throughout the migratory period. Correcting for turnover places the total population of shorebirds using the intertidal area of the Bay of Fundy somewhere in the range of 800,000 to 1,400,000 birds, 95% of which are Semipalmated Sandpipers.

The wide range reflects variations in peak numbers of Semipalmated Sandpipers between years and between roost sites. Richardson (1979) has shown, with the aid of radar, that although large flocks of shorebirds stopped in Fundy during southward migration, many flocks passed over central new Brunswick and continued in a southeasterly direction over the ocean. This suggests that many shorebirds are able to accumulate sufficient fat reserves at staging areas north of Fundy to continue directly over the Atlantic Ocean, presumably to the wintering grounds. The numbers that do so, however, may vary depending on the quality and quantity of available food resources at staging areas, which may fluctuate between years. Brousseau (1981) showed that approximately 80,000 sandpipers congregate in the St. Lawrence River, and large flocks also gather on the Magdalen Islands in the Gulf of St. Lawrence (McNeil and Cadieux 1972). McNeil and Cadieux (1972) reported that although large numbers of the Semipalmated Sandpipers on the Magdalen Islands had sufficient lipid reserves to fly a distance of 3200 km, many others departed with low fat

TABLE 6

COMPARISON OF POPULATION ESTIMATES FOR NINE SPECIES OF SHOREBIRDS STOPPING IN THE BAY OF FUNDY IN AUTUMN

Method	Single-day peak numbers (adults)	Peak numbers adults + immatures	Total population estimate[a]
1976 aerial survey	566,000		1,554,143[b]
1976 ground survey	564,312		705,390–1,129,000
Summation of average peak numbers of adults (1974–1983)	598,666		748,333–1,197,000
Summation of average peak numbers of adults and immatures (1974–1983)		694,093	867,603–1,388,166

[a] Range refers to 1.25 to 2 times as many birds as single-day peak count to account for turnover (see Methods).
[b] Summation of results from 10 aerial surveys over 8-week period (19 July–12 September 1976).

levels which would have had to be replenished elsewhere before undertaking a transoceanic flight to South America. Hence, in some years, more birds may fly from the St. Lawrence River or the Magdalen Islands to the Bay of Fundy before continuing to the wintering areas if food resources at the more northern staging areas were reduced.

That possibility is supported by banding and color-marking information. Semipalmated Sandpipers color marked in James Bay (Morrison and Gratto 1979), the Magdalen Islands (McNeil and Burton 1977), the St. Lawrence River (P. Dupuis, pers. comm.), and the coast of Maine (T. May, pers. comm.) were seen in the Bay of Fundy the same year they were color marked. The sandpipers that were marked in southeastern Maine flew north to feeding grounds in Chignecto Bay in the upper Bay of Fundy. The "funneling" of sandpipers to the Bay of Fundy from other staging sites contributes to its importance as a major foraging area for migrant shorebirds during the southward migration.

Spaans (1979) indicated that shorebirds in Suriname arrived "one to two weeks" after they were first seen in the Bay of Fundy. If this statement specifically means a period of 7 to 14 days, it suggests a faster turnover rate than the 10 to 20 days I have used here. However, those birds that arrived in the Bay of Fundy, and might have stopped previously along the Saint Lawrence River in Quebec or on the Magdalen Islands in the Gulf of St. Lawrence, would be expected to use the Bay of Fundy for a shorter period to "top off" their fat reserves prior to a long-distance flight. Sandpipers which might have flown to the Bay of Fundy directly from the Arctic breeding grounds presumably would arrive leaner and have to

stay longer. As I am unable to distinguish between these groups, a length of 15 days appeared most reasonable, as it would accommodate all weight classes at arrival. Hence, my estimates based on a 15-day turnover rate must be regarded as conservative until further research can determine the length of stay of specific individual birds of known arrival-departure dates and weights.

Recently, Morrison (1983) and Morrison et al. (1985) estimated the wintering population "of small shorebirds (mainly Semipalmated Sandpipers)" along the northern coast of South America at 1.9 million birds. Of those, 70% were seen in Suriname, 20% in French Guiana, and 0.5% in Guyana. These areas are most likely the wintering areas of those birds seen each autumn in the Bay of Fundy. On 6 June 1978, Boates (1980) collected a Semipalmated Sandpiper in the Southern Bight, Minas Basin, that had been banded near Paramaribo, Suriname, on 13 May 1976. In August of the same year, I saw 4 color-banded Semipalmated Sandpipers in Shepody Bay which had also been banded by Spaans in Suriname during 1976 and 1977 (A. Spaans, pers. comm.). On 11 August 1981, I recovered a band near Cumberland Basin from the leg of a Suriname-banded Semipalmated Sandpiper killed by a domestic cat on that date. Two Semipalmated Sandpipers banded in 1981 at Dorchester Cape were subsequently recovered in Guyana. One of these was found there the same month it was banded in the Bay of Fundy. Morrison (1984) reported that of 40,000 Semipalmated Sandpipers banded in James Bay between 1974 and 1982, 60 of 66 band recoveries from Guyana, Suriname, and French Guiana occurred in Guyana even though only a small proportion of over-wintering birds are found there. He attributed the high rate of band recoveries in Guyana to the greater accessibility of the coastline to people plus the practice of hunting shorebirds for food in that country during the birds' migration to Suriname and French Guiana. This may explain why the recoveries of the two sandpipers banded in the Bay of Fundy were in Guyana and not in Suriname as Morrison's (1984) survey data, and the banding observations noted above, would suggest.

Of the 1.9 million sandpipers estimated to winter in those three countries, my estimates for the Bay of Fundy (Table 5) represent 42–74% of that total.

Lack of information on the size of North American populations of shorebirds makes it difficult to assess quantitatively the relative importance of the Bay of Fundy to these populations in a continental context. For example, the number of Black-bellied Plovers may reach 10,000 in the Bay of Fundy during fall migration. This represents nearly 50% of the total number estimated for all of Britain (Moser 1987), equivalent to 20% of the European population (Cramp and Simmons 1983), but this may

be proportionally less significant with regard to the New World population. Spaans (1978) estimated that between 2500 and 50,000 Black-bellied Plovers occur throughout the year in Suriname. He also estimated numbers of Short-billed Dowitchers along the Suriname coast at 100,000 or more. Therefore, the numbers of dowitchers in the Bay of Fundy would represent 8.5% of the Suriname estimate at most. Similar comparisons for Semipalmated Plover and Least Sandpiper in the Bay of Fundy amount to 44% and 18%, respectively, of the population estimates made by Spaans (1978) for the Suriname coast. For Red Knot, the maximum of 1700 birds estimated in the Bay of Fundy amounts to about 1.0% of the nearly 150,000 Morrison (1984) estimated as the total New World population.

Except for the Black-bellied Plover, the spring migration of shorebirds in the Bay of Fundy is not significant. The few Semipalmated Sandpipers, Semipalmated Plovers, and dowitchers seen in spring probably represent birds that have strayed from a more commonly used inland route. Dunne et al. (1982) showed that in late May very large numbers of Semipalmated Sandpipers (nearly 175,000 on 21 May 1982) congregate in Delaware Bay, and as many as 25,000 have been seen in Cape Cod on 30 May (Hill 1965) and 35,000 on 1 June, 1957 (Bailey 1968 in Harrington and Morrison 1979). As only a small proportion of these numbers reaches the Bay of Fundy in late May and early June, the large flocks in Delaware Bay probably fly west-northwest towards the breeding grounds, thus bypassing the Bay of Fundy altogether. Dunne et al. (1982) did not report Black-bellied Plovers in Delaware Bay in spring as one of the "principal" migratory species, although Bailey (1955) mentioned peaks of 2000 to 2500 in Massachusetts. As single flocks of nearly 1400 Black-bellied Plover have been recorded in the Bay of Fundy in late May and early June, part of the population appears to follow a coastal route northwards to the Maritime Provinces.

During April and May, the densities of invertebrates in mud and sandflats in the Bay of Fundy are very low owing to severe ice-scouring throughout the winter months (Hicklin et al. 1980, Gordon and Desplanque 1983, Gordon et al. 1985). The resulting lack of food in spring may be partly responsible for the low use of the area by migrant shorebirds at this time. Consequently, Black-bellied Plovers in the Southern Bight during May and June foraged on the more elevated salt marshes where they preyed on the larvae of soldier and horse flies (Order Diptera). Conversely, in late summer and fall when food was more abundant, they confined their foraging activities to mudflats and primarily consumed polychaetes (Hicklin and Smith 1979).

The main passage of the seven major species examined in this paper occured during a five-week period beginning the last week of July. The

Sanderling and Dunlin are high arctic breeders that undergo a partial molt on the breeding grounds and leave the breeding areas much later.

The migration of shorebirds in the Bay of Fundy in late July and August coincides with the period of maximum invertebrate production, notably the 5 mm long amphipod *Corophium volutator* (Peer et al. 1986), which is a main prey of Semipalmated Sandpiper, Least Sandpipers, Short-billed Dowitchers, and Semipalmated Plovers (Hicklin and Smith 1979, 1984). An abundance of food in the Bay of Fundy at this time is probably the main factor for the strategic importance of this area to migratory shorebirds along the eastern seaboard, notably the very large population of Semipalmated Sandpipers. Throughout the migratory period, foraging sandpipers concentrate on mudflats where *Corophium* is most abundant (Hicklin and Smith 1984). Boates (1980) has shown that Semipalmated Sandpipers ingest between 9600–26,100 *Corophium*/bird/day, depending on tide height and the amount of time the flats are exposed in daytime. During the period that shorebirds are present in the bay, *Corophium* production from July to September is between 3.8 and 5.2 g dry weight/m^2 of mudflat at Pecks Cove, Cumberland Basin (Peer et al. 1986), a site of relatively low shorebird abundance (Hicklin, unpubl. data) to 22.0 g dry weight m^2 at Avonport Beach, Minas Basin (Gratto 1979), a major foraging area used by Semipalmated Sandpipers (Hicklin and Smith 1984).

The high biomass of food present each year during July and August would allow birds to put on the necessary fat stores to complete their migration to South America by an overseas route. In extreme cases, some sandpipers in Fundy attain weights in excess of 50 grams, which can impede the birds' ability to fly (Hicklin, unpubl. data), and represents 51% of body mass above fat-free weight (24.5 $\pm$ 2.3 grams, both sexes combined), presumably in the form of fat (Hicklin, unpubl. data). On average, 10 days following the onset of migration into the bay, 30% of the roost at Dorchester Cape consists of sandpipers weighing over 40.1 grams ($\bar{x}$ = 43.2 grams) for an average fat content of 17.3 grams (N = 31) or 40% of the fresh weight (Hicklin, unpubl. data). By using the methods in McNeil and Cadieux (1972) to calculate flight ranges, one can predict that these birds would have a flight range capability of 4400 km, or sufficient energy stores to fly directly from the Bay of Fundy to the northern coast of South America, a distance of about 4300 km.

The combination of wide intertidal flats and an abundant food supply in late summer in the Bay of Fundy allows for the large populations of birds described in this paper to stop in the bay and deposit fat stores prior to the long flight to their wintering areas. These attributes of the Bay of Fundy make it one of the more significant shorebird stopover areas during autumn migration along the eastern seaboard of North America.

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Appendix 1

Average Peak Numbers of Shorebirds at Miscellaneous Sites in the Bay of Fundy

Sites	Species								
	Black-bellied Plover	Semi-palmated Plover	Red Knot	Sanderling	Semi-palmated Sandpiper	Least Sandpiper	White-rumped Sandpiper	Dunlin	Dowitcher
Cheverie (2)[a]	500	173	0	36	4950	0	3	35	0
Moose Brook (2)	25	76	0	0	2813	5	1	0	0
Noel Bay (5)	57	1876	0	3	4450	16	19	3	8
Noel Shore (4)	82	11	0	0	5500	0	0	1	3
Noel Point (4)	44	85	3	1	1238	0	1	43	5
Sterling Brook (3)	65	42	0	0	2300	25	0	0	1
Shubenacadie (2)	13	20	0	0	600	75	0	0	2
Highland Village (3)	93	400	0	15	4500	125	0	6	1
Economy (3)	200	200	1	150	1333	50	35	17	1
Five Islands (1)	0	0	0	0	0	0	0	0	0
Minudie (6)	—	—	—	—	30,000	—	—	—	—
Hopewell (3)	—	—	—	—	60,000	—	—	—	—
John Lusby (2)	5	225	0	0	100,000	200	1	0	100
Missaquash (1)	0	0	0	0	1	1	0	0	100
Tantramar River (1)	0	35	0	0	2900	100	0	0	50
Waterside (7)	4	46	5	73	196	34	4	3	21
Quaco Bay (5)	29	731	0	527	1067	554	2	0	32
Manawagonish Marsh (1)	70	303	0	0	8984	3150	600	1	951
Dipper and Chance Harbours (2)	13	43	1	28	168	99	6	5	1
Maces Bay (3)	107	1340	0	118	3690	1763	82	2	184
Courtenay Bay (2)	39	188	0	5	6500	7	0	8	230
Kent Island (3)	77	423	2	30	2983	417	74	1	370
St. Andrews (1)	10	300	1	0	10	2	5	0	0
Grand Manan (6)	185	344	29	60	3526	275	23	35	108

Appendix 1
Continued

Sites	Species								
	Black-bellied Plover	Semi-palmated Plover	Red Knot	Sanderling	Semi-palmated Sandpiper	Least Sandpiper	White-rumped Sandpiper	Dunlin	Dowitcher
Point Lepreau (1)	16	580	0	11	1005	250	45	0	72
Saints Rest Marsh (1)	3	1000	20	10	20,000	300	2	0	150
Portapique River (3)	1	25	0	0	125	2	0	0	0
Bass River (3)	0	8	0	0	60	5	0	0	0
Little Dyke (3)	6	545	10	30	3488	23	0	10	4
Lyon's Head (1)	30	150	43	10	2000	15	0	0	4
Black Rock (3)	27	63	17	6	500	25	0	0	1
Total	1701	7543	132	1114	274,887	7518	903	170	2299

[a] Numbers in parentheses refer to number of years counts were made.

Wilson Bull., 99(4), 1987, pp. 571–578

SPRING SHOREBIRD MIGRATION THROUGH CENTRAL VENEZUELA

BETSY TRENT THOMAS[1]

ABSTRACT.—Nearctic-breeding shorebirds regularly migrate through the llanos of central Venezuela in the spring (March–May). At a single site, consisting of three feeding areas with a total of 3–5 ha, 10 species were recorded. Four migrating Least Sandpipers (*Calidris minutilla*) banded at this site were recaptured there in subsequent years. White-rumped Sandpipers (*C. fusicollis*) dyed and flagged in the Venezuelan llanos were observed a few weeks later, one in Texas and two in Kansas. Shorebird weights, numbers, passage times, and lengths of stay at the study site are given. Nearly all shorebirds had recently completed molt of remiges and rectrices, but none were in distinctive breeding plumages or colors.
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Although shorebird migration routes are relatively well known in North America, their passage routes in South America, where most species spend over half of their lives, are poorly understood. Recently, interest has increased in the welfare of migrant nearctic-breeding shorebirds because feeding and resting sites are limited and declining in both number and quality (Myers 1983, Senner and Howe 1984).

I briefly sampled spring shorebirds on migration at a single site in 1982 and 1983. In 1983 I recaptured one of the 21 Least Sandpipers (*Calidris minutilla*) banded in the previous year. Because of this I decided to study in detail shorebird passage in 1984. Here, I give data on species, passage times, numbers, weights, molt, length of stay, and returns.

STUDY AREA AND METHODS

The site of most observations and all mist-netting was a 4000-ha cattle ranch, Fundo Pecuario Masaguaral, approximately central in the llanos of Venezuela (08°31′N, 67°35′W). A description of the vegetation of this ranch is in Troth (1979). Masaguaral, 45 km south of Calabozo in the state of Guárico, is about 240 km inland from the nearest maritime shore on the Caribbean Sea and separated from it by the Coastal Range of mountains. The llanos, covering much of the center of Venezuela (approximately 200,000 km^2), are natural grassland savannas, intersected by large, broad rivers such as the rios Orinoco, Portuguesa, Apure, and Meta. A similar-sized savanna with generally the same edaphic conditions lies to the southwest in Columbia (Huber 1974). The savannas of both countries, (2°–10°N, 30–200 m elevations) are hot with small annual temperature variation. The year is roughly divided into wet and dry seasons.

On Masaguaral three deep-well pumps run continuously throughout the dry season to keep two marshes and one lagoon wet for wildlife. Shorebirds used a maximum of only 5 ha, because the marshes varied in size within and between years, and much of the lagoon

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edge was unsuitable for them. I mist-netted at one 1.5 ha marsh and at the 3 ha lagoon area. Most netting was done in the early morning and late afternoon to avoid a strong wind from 09:00 to 16:00 in the dry season. I worked on 6 days in April and early May in 1982 (60 mist-net hours), and 6 days in April 1983 (134 mnh). During 1984 I netted shorebirds on 44 days (912 mnh) from 20 March–19 May, covering the principal time of shorebird passage.

Captured birds received standard U.S.F.W.S. leg bands and after 23 April 1984, most were also marked with black plastic leg flags and picric acid dye on the right ventral surface, using guidelines of the Pan American Shorebird Program (Myers et al. 1983). Each bird was weighed to the nearest 0.1 g and 1 g respectively, using 50-g and 100-g Pesola spring balances which were checked for accuracy at least once a day. Most shorebirds were released within 20 min of capture.

I counted shorebirds at all three wet areas on the ranch to define their presence and numbers. Data were divided into 10-day periods each month (early, mid, and late). To compare the three most common species' abundance and timing, I used only those counts in 1984 from the 3 ha lagoon area, listing the single highest count on days when I made an early morning and late afternoon count. A few observations used from other years are noted.

Later I examined all of the 10 shorebird species found at the study site, in both the Colección Ornithológica Phelps, Caracas, and in the American Museum of Natural History, New York. My objective was to record all interior Venezuelan spring migration dates, sites, and abundance as represented in those collections.

RESULTS

Species, passage months, and numbers.—I found 10 species of nearctic-breeding shorebirds at Masaguaral during northward migration: Greater Yellowlegs (*Tringa melanoleuca*), Lesser Yellowlegs (*T. flavipes*), Solitary Sandpiper (*T. solitaria*), Spotted Sandpiper (*Actitis macularia*), Semipalmated Sandpiper (*Calidris pusilla*), Least Sandpiper, White-rumped Sandpiper (*C. fusicollis*), Pectoral Sandpiper (*C. melanotos*), Stilt Sandpiper (*C. himantopus*), and Buff-breasted Sandpiper (*Tryngites subruficollis*). Small numbers of four other shorebird species have been found in the eastern Venezuelan llanos (Phelps and Phelps 1958, Meyer de Schauensee and Phelps 1978), but I have never seen any of them on this ranch during 14 years of observations. Black-necked Stilts (*Himantopus mexicanus*), recorded on Masaguaral January–June (Thomas 1979), migrated through from early April through May in small numbers (maximum daily count 18). McNeil (1971) found them breeding in eastern Venezuela; thus there is no certainty that these individuals were not just making local movements, and I do not consider them further in this paper.

With the exception of fewer than 10 Solitary Sandpipers and 5 Spotted Sandpipers that usually spend the northern winter on the ranch each year (Thomas 1979), all other shorebirds and most Solitary and Spotted Sandpipers were transients; no shorebirds were ever found "summering" (McNeil 1970) on the ranch.

From 1982 to 1984 the pattern of migration was the same. The earliest

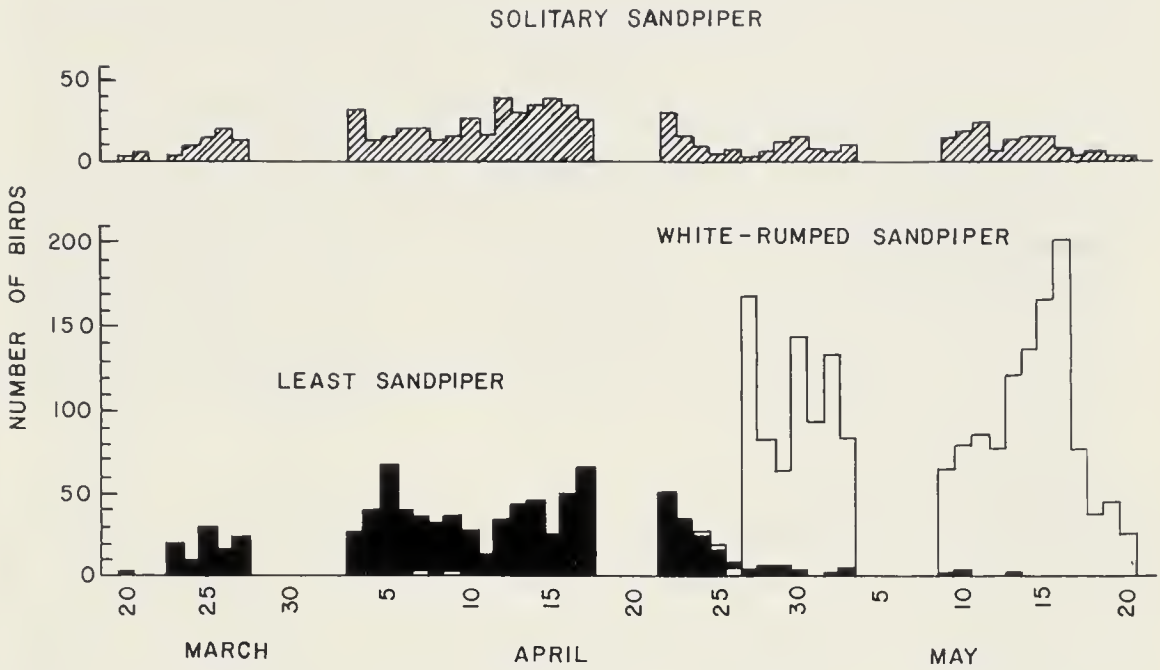

FIG. 1. Shorebird counts during northward migration in 1984 at a 3-ha artificially flooded site in the Venezuelan llanos.

arrivals were Greater Yellowlegs (maximum daily number = 2) from late February through early April. Lesser Yellowlegs passed from mid-March through mid-May, with peak daily numbers of 7 in early April. Transient Solitary Sandpipers appeared from late March to mid-May. Least Sandpipers and small numbers of Semipalmated Sandpipers passed through from late March to early May. A few White-rumped Sandpipers were seen in mid-April but most birds came through between late April to mid-May. Spotted Sandpiper migrants were last, passing through from late April to late May (maximum daily count in mid-May = 5). Three additional species were found in small numbers: Pectoral Sandpipers were present irregularly from mid-April to early May (maximum = 5); Stilt Sandpipers were present occasionally (1–4) between mid-April and mid-May (maximum = 4), with a flock of 19 on 20 April 1985. A single Buff-breasted Sandpiper was netted on 26 April 1983. The two most abundant species, Least and White-rumped sandpipers, overlapped only briefly (Fig. 1).

Least Sandpiper numbers, which were generally stable during the daytime, sometimes changed substantially overnight, suggesting fall-out of nocturnal migrants. White-rumped Sandpipers, however, appeared to pass over during daytime. On all eight days when I censused the birds early in the morning and late in the afternoon, White-rumped Sandpiper numbers had increased (9–44%). White-rumped Sandpiper also was the only

TABLE 1
SHOREBIRD WEIGHTS AT FIRST CAPTURE (ALL YEARS COMBINED)

Species	Number captured	$\bar{x} \pm$ SD (range)
Lesser Yellowlegs	3	82.40 (74.0–93.0)
Solitary Sandpiper	104	48.40 ± 8.56 (31.1–65.1)
Spotted Sandpiper	11	37.12 ± 4.00 (32.9–46.0)
Semipalmated Sandpiper	19	24.46 ± 3.82 (18.2–31.2)
Least Sandpiper	276	23.20 ± 3.56 (16.0–34.0)
White-rumped Sandpiper	367	34.69 ± 4.55 (27.5–45.7)
Pectoral Sandpiper	3	53.00 (47.3–57.2)
Stilt Sandpiper	1	63.20
Buff-breasted Sandpiper	1	38.10

species that I saw leaving the study area diurnally in discrete flocks. These birds typically stopped feeding, rested in unusually tight flocks, then flew up together as a calling group, circled several times overhead, and departed north northwest (compass direction of approximately 330°).

Weights and molt.—There was a broad weight distribution in most species due to both sexual size dimorphism and migratory fat deposits (McNeil 1970, Prater et al. 1977, Johnsgard 1981, Dunning 1984) (Table 1). Weights of repeat birds of three species in 1984 (N = 39) generally showed a gain, although some lost weight in the early days after initial capture and gained weight on longer stays (Table 2), much as Page and Middleton (1972) found in migrating Semipalmated Sandpipers at an Ontario stopover.

All birds were examined for molt. Most individuals of all species had new flight feathers and old (worn and fringed) dorsal contour feathers. Exceptions were birds that had not completed rectrix molt. I did not determine the ages of birds. No birds were in breeding colors such as the distinctive breeding plumage described by Blake (1977) for Stilt Sandpipers, and soft part colors for Spotted Sandpipers (Prater et al. 1977).

Returns and sightings.—Although only 75 Least Sandpipers were banded in 1982 and 1983, there were four returns (5%). Three returned one year later, less 2, 7, and 8 days from their original capture dates. The fourth Least Sandpiper returned two years plus 4 days after its first capture. One Least Sandpiper netted on 19 April 1982 had been banded as a juvenile 5 September 1981 in Westboro, Massachusetts.

I began dying and flagging shorebirds on 23 April 1984; thus most dyed birds were White-rumped Sandpipers (Fig. 1). Observers cooperating with the Pan American Shorebird Program reported three of these in North

TABLE 2
MEAN STOPOVER DURATION BETWEEN CAPTURES AND MEAN WEIGHT GAIN OF SHOREBIRDS IN THE VENEZUELAN LLANOS DURING SPRING MIGRATION 1984

Species (N)	Mean stopover time	Mean change in weight
Solitary Sandpiper (7)	5.1 ± 3.3 (1–9)[a]	0.64 ± 2.6 (−6.8–+8.6)
Least Sandpiper (21)	11.2 ± 8.4 (1–31)	2.89 ± 3.5 (−4.7–+9.9)
White-rumped Sandpiper (11)	4.5 ± 5.7 (1–11)	4.47 ± 4.5 (−2.1–+11.2)

[a] Mean number of days ± SD (range).

America, in the same migratory season. One bird was seen on 14 May at San Angelo, Texas, and two others were seen on 23 May at Cheyenne Bottoms, Kansas. These birds were certainly from Masaguaral, because I was the only worker in Venezuela using dye and black flags on shorebirds that season.

DISCUSSION

Site fidelity of nearctic shorebirds to migration stopover areas had been observed in Semipalmated and Western (*C. mauri*) sandpipers (ffrench 1973), Spotted Sandpipers (McNeil 1982), Red Knots (*C. canutus*) (Harrington and Twichell 1982), Sanderlings (*C. alba*), Ruddy Turnstones (*Arenaria intrepes*) (Myers, unpubl. data), and Semipalmated Plovers (*Charadrius semipalmatus*) (Smith and Houghton 1984). This paper shows that Least Sandpipers share this characteristic behavior.

The time of spring shorebird passage (March–May) coincides with the end of the dry season when the llanos are usually parched and bare. In some years, however, due to the variable beginning of the annual rains (Thomas 1985), shorebirds are present during the earliest rains. The only extensive natural water during spring migration is along the rivers in large sandbars and a few mud flats. An additional, but unpredictable, source of shallow water is in newly created (since 1955) rice fields in the northern Venezuelan llanos. These fields were used by shorebirds occasionally when they were fallow and slightly irrigated for pasture, or immediately after rice seeding. In some years many hectares were available during shorebird passage, and in other years none had water at this time. Usually, however, the total of 3–5 ha of shorebird feeding habitat at Masaguaral is a tiny oasis in a vast and generally inhospitable habitat.

During the three years of the study, the order in which the different species stopped over at Masaguaral was consistent, even though the conditions of feeding sites varied. In 1982 the most heavily used area was a 1.5-ha shallow, clearwater pond flooded by water pumped over a field

which had suffered a grass fire four weeks before migration time. In 1983 and 1984 there was little or no water at this site, and the birds foraged mainly on 3 ha of mud flats 1.5 km away on the edge of a lagoon maintained in the dry season by pumped water. In 1985 heavy early rains left abundant shallow water throughout the llanos and fewer shorebirds stopped at Masaguaral during April–May. I believe this was because transient birds used natural foraging sites.

During the northern summer (July–September) no shorebirds stayed on the ranch, probably because at that time much of the land is flooded with seasonal water often too deep for foraging. The "summering" individuals that McNeil (1970) found at his northeastern coastal study area were there because the maritime shore remains hospitable throughout the year. A few early fall migrants occasionally stopped over briefly on Masaguaral (August–October) but numbers were low (5–10 birds), and they stayed less than a day, usually in years when low rainfall exposed a few mud foraging areas.

No previous studies have been made of inland migrating shorebirds in Venezuela, and H. Sick (pers. comm.) knows of no study from Brazil. Thus shorebird migration through interior continental South America is known from opportunistically observed or collected birds in museums. There were few birds from interior Venezuelan sites March–May in the two museum collections I examined (i.e., Least Sandpiper 3, 2 [first figure from the Colección Phelps, second from AMNH]; White-rumped 3, 1; Pectoral 1, 0; Stilt 0, 0; Buff-breasted 11, 4). All of the Buff-breasted Sandpipers in both collections were from the Territory Amazonas, 300–700 km south of my study site. The literature, which is based on museum collections (Phelps and Phelps 1958, Blake 1977, Meyer de Schauensee and Phelps 1978), does not suggest the extensive spring migration through Venezuela that I found.

Studies of nearctic shorebirds in South America have concentrated on discrete coastal areas of the continent (McNeil 1970, 1982; Spaans 1978; Myers and Myers 1979; Harrington et al. 1986). Although it is well known that vast numbers of shorebirds pass along the Mississippi flyway through continental North America (Johnsgard 1981), perhaps because there is no major north-south river valley in South America, interior migration on this continent has been largely ignored. Additional, long-term, study of interior South American shorebird migration will give a clearer understanding of the extent and importance of this migration route.

ACKNOWLEDGMENTS

I thank T. Blohm who maintained water pumps for many years before he learned that migrant shorebirds used those sites. I also thank M. Howe who came to Venezuela with

flags and dye and worked with me for ten days during peak migration in 1984. T. Maxwell and E. Martinez were the alert observers of the dyed White-rumps in the U.S. I appreciate the assistance of the curators and staffs of the Colección Phelps and the American Museum of Natural History, as well as the help of J. Trent, O. Huber, S. Senner, B. Dickerman, J. Ogden, C. Collins, S. Alstead, and F. Sunquist. Colleagues who kindly reviewed and improved the manuscipt were M. Howe, P. Myers, B. Harrington, J. Eldridge, E. Burtt, R. McNeil, and K. Bildstein.

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CENTENNIAL MEETING IN PHILADELPHIA, PENNSYLVANIA, 9–12 JUNE, 1988

The Wilson Ornithological Society will hold its Centennial Meeting from 9 to 12 June 1988 at Rosemont College in suburban Philadelphia, Pennsylvania. A three-day scientific program (one day more than customary) is scheduled, with contributed papers and symposia. Morning field trips are planned as well as day trips on Sunday, June 12. Tours of interest will be scheduled for non-ornithological spouses and guests. Centennial Day, including an international symposium on *Parus* and a gala reception, will be at the Academy of Natural Sciences of Philadelphia. The meeting announcement and call for papers will be mailed to members in early January, 1988. Queries may be directed to: WOS Local Committee, Department of Ornithology, Academy of Natural Sciences, 19th and The Parkway, Philadelphia, PA 19103.

Wilson Bull., 99(4), 1987, pp. 579–600

THE BIRDS OF CAT ISLAND, BAHAMAS

DONALD W. BUDEN[1]

ABSTRACT.—Ninety-seven species of birds are recorded from Cat Island and immediately adjacent cays, 46 for the first time. No species or subspecies is endemic. Of the 47 probable breeding species, 23 are land birds (exclusive of hawks and the introduced Rock Dove [*Columba livia*]); 24 and 26 are predicted from island size and rainfall data, respectively. Nests, eggs, and young are reported for 27 species, 25 of them recorded breeding on Cat Island for the first time. Most of the indigenous breeding land birds are widespread in all terrestrial habitats; habitat preferences are pronounced in several. Most of the breeding species are widespread in the Bahamas generally, but the Bahama Yellowthroat (*Geothlypis rostrata*) and Red-legged Thrush (*Turdus plumbeus*) are not known to breed in the archipelago south of Cat Island. The resident race of the American Kestrel (*Falco sparverius*) is near the northern limits of its range there. The Bahama Mockingbird (*Mimus gundlachii*) is the most abundant land bird. *Received 17 Dec. 1986, accepted 20 Mar. 1987.*

Ornithologically, Cat Island is one of the least known among the main islands of the Bahamas. Its avifauna has never been reviewed systematically, previous reports being largely noncumulative lists of species with few annotations. The present study brings up-to-date all information on the distribution and status of the birds of Cat Island, including several offshore cays. It is based in large measure on my observations during 23 May–28 July 1986.

STUDY AREA

Cat Island (92 km long, 389 km^2; Ministry of Education 1985) is on the eastern side of the Great Bahama Bank, roughly in the middle part of the Bahama archipelago (Figs. 1 and 2). It is fringed by both rocky and sandy beaches, and by cliffs that reach ca 60 m high on the southern coast; no part is more than 4 km from the sea. Mount Alvernia (elev. 67 m), just inland from New Bight, is the highest land in the Bahamas. Small settlements (total population 2657; Ministry of Education 1985) and several resort and housing complexes occur on the western coast and at the southern end. A paved road connects all settlements, and several dirt roads and many footpaths traverse the island.

Climatological data for New Bight for the years 1952–1962 are given by Lind (1969). The average monthly temperatures ranged from 22.2°C in January to 28.3°C in August, the mean annual temperature being 25.6°C. Rainfall averaged 995.7 mm/year, with January and February the driest months (30.5 mm each) and September and October the wettest (231.1 mm each).

The vegetation on Cat Island is predominately scrubland and xeric-to-semimesic broadleaf woodland growing in shallow soils or directly on a limestone base pockmarked by caves and sinkholes. A long history of slash-and-burn agriculture has created a patchwork of 1–2 acre (occasionally larger) plots, which are either under cultivation or in different stages of

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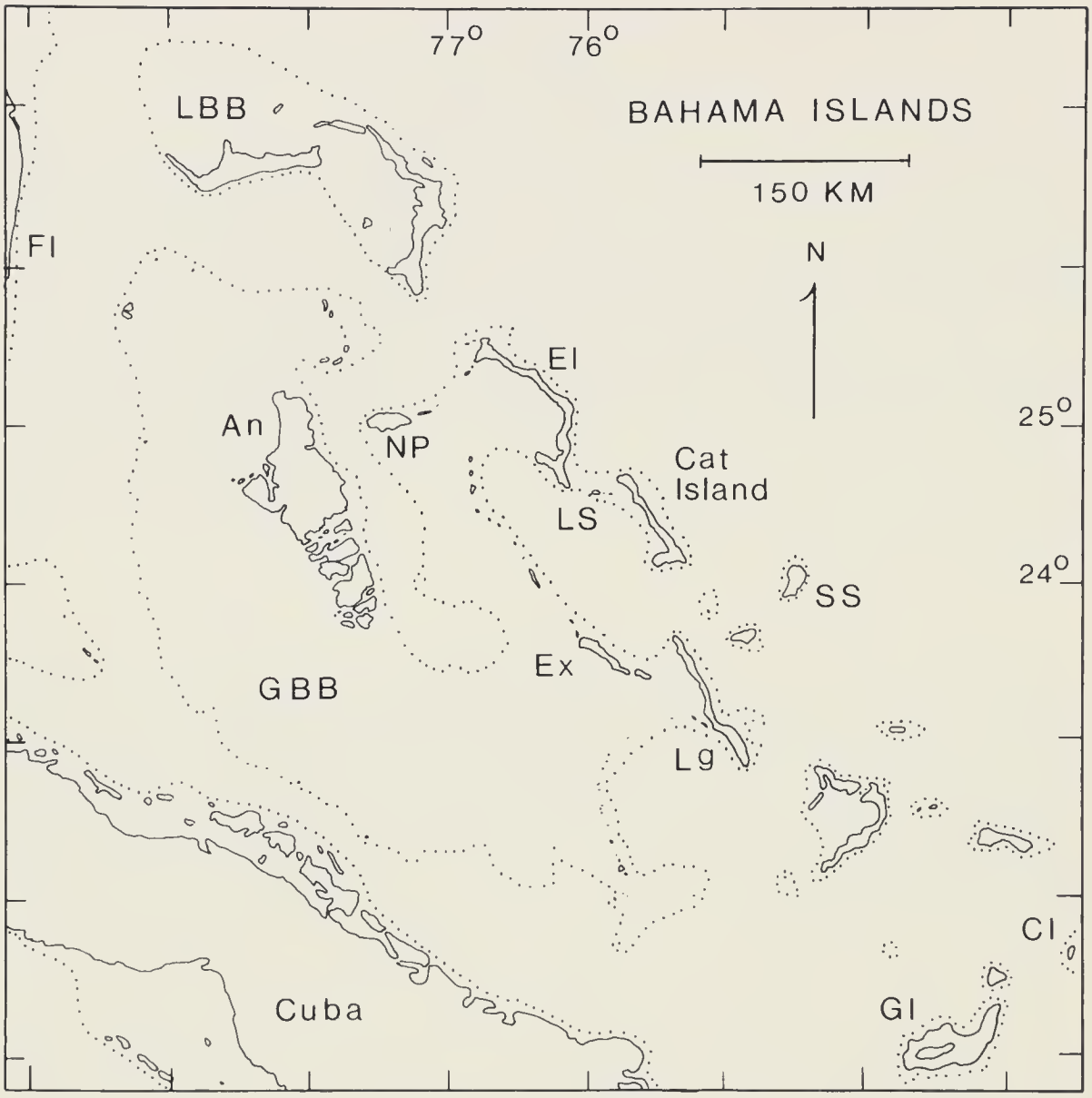

FIG. 1. Map showing the location of Cat Island and other Bahama Islands; dotted lines denote the 100-fathom contour. An = Andros, CI = Caicos Islands, El = Eleuthera, Ex = the Exumas, Fl = Florida, GBB = Great Bahama Bank, GI = Great Inagua, LBB = Little Bahama Bank, Lg = Long Island, LS = Little San Salvador, NP = New Providence, SS = San Salvador.

secondary succession. For the most part, the tallest trees (10–15 m) and the most extensive woodlands are on the sheltered slopes of the mainly north-south ridges. Stands of casuarinas (*Casuarina equisetifolia*) occur on the coast, being most numerous on the western side of the island. Mangroves are common in tidal creeks and along the shores of salt ponds, and small, temporary to semipermanent freshwater ponds, swamps, and marshes occur throughout. A comprehensive review of the vegetation is given in Byrne (1980).

ORNITHOLOGICAL HISTORY

The earliest surveys of the avifauna were made during wide-ranging expeditions that stopped only briefly on Cat Island: the *Albatross* Expedition, 11 March 1886 (Ridgway

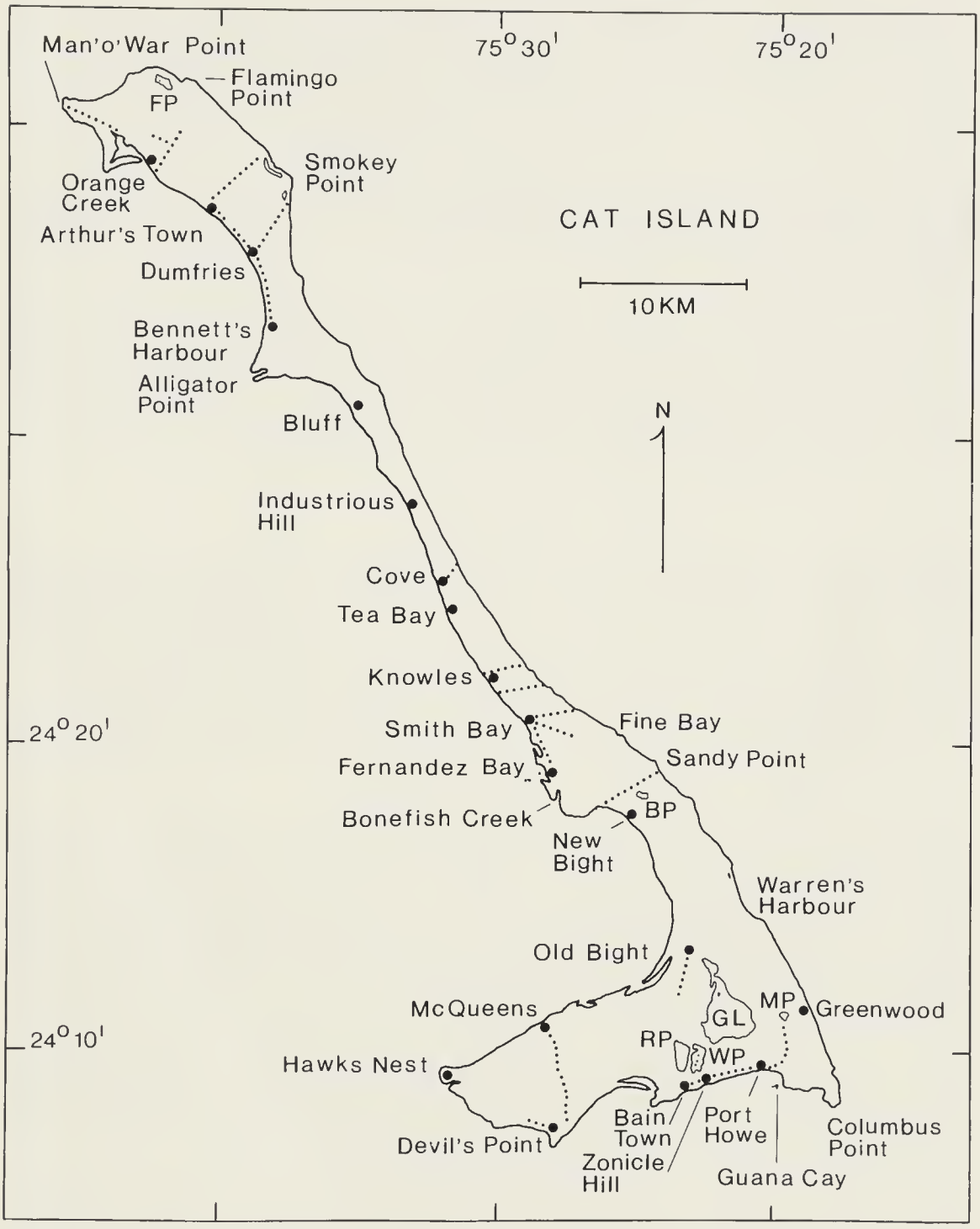

FIG. 2. Map of Cat Island. Large dots indicate settlements and resort-housing complexes; dotted lines show routes followed on census walks. BP = Brine Pond, FP = Flamingo Pond, GL = Gambier Lake, MP = McKinney Pond, RP = Red Pond, WP = White Pond.

1891); the Geographical Society of Baltimore Expedition, 9 July 1903 (Riley 1905); and the Carnegie Museum Expedition, 25–26 January and 6–7 April 1909 (Todd and Worthington 1911). Additionally, several specimens were collected by J. Percy Moore in November 1890 and deposited in the Academy of Natural Sciences of Philadelphia (M. Robbins, in litt.).

Paulson (1966) added 17 species to the birds known from Cat Island, based on his

observations during 27 November–2 December 1963, and he presented additional records for five others, thus providing the most comprehensive previous report on the avifauna. Schwartz (1970) reviewed *Geothlypis rostrata* and listed all the specimens known from Cat Island. The only other reports on the birds of Cat Island appear to be the brief comments and several new records mentioned in supplements to Bond's check-lists of West Indian birds (Bond 1951, 1957, 1959, 1978, 1980, 1982) and one questionable sight record of *Rissa tridactyla* (see Norton 1984). Also, Sprunt (1984) recorded *Sterna anaethetus* nesting on Port Howe Rock (=Guana Cay). Undated sight records by R. W. Hanlon (in Bond 1959) presumably are for 1958.

Many new locality records in the present study were contributed by James Perran Ross and Sarah Fay Baird who visited Cat Island in April, May, August, and December 1982. See Acknowledgments for other contributors. Specimens that I collected during a brief visit on 2 and 3 March 1968 and those collected by Paulson in 1963 were deposited in the Albert Schwartz Collection (Louisiana State University Museum of Zoology). Those that I collected in 1986 are in the Museum of Comparative Zoology, Harvard University.

METHODS

English names and binomials are those of the American Ornithologists' Union (1983). Subspecies are mentioned only in selected cases and are from Bond (1956), unless indicated otherwise. Abbreviations of names of observers are AS = Alexander Sprunt, DWB = Donald W. Buden, JPR and SFB = James Perran Ross and Sarah Fay Baird, and PM and MM = Peter and Madeleine Mann. Abundance is based largely on numbers of individuals usually seen during a day in the field: VC = very common, 30 or more/day; C = common, 15–30/day, FC = fairly common, 5–15/day, UC = uncommon, 1–5 on most days but not seen every day; S = scarce, 5–15/season; and R = rare, 1–5/season.

Residents occur year-round and breed on the island; summer visitors breed on the island but are less numerous or absent in winter. Nonbreeding visitors are mainly winter visitors and transients from continental North America, but include birds that occur in smaller numbers throughout the summer but do not breed, birds that are known to breed on other Bahama Islands, and those that are occasional visitors or vagrants to the Bahamas generally. Introduced birds are those established on the island by humans. In view of the brief and scanty winter surveys—and only one extensive summer survey—I have not attempted to distinguish among the different kinds of nonbreeding visitors. That many herons and shorebirds are unrecorded during autumn, winter, and spring, for example, almost certainly is an artifact of sampling. In some cases where records for Cat Island are especially scanty, "probable" or "possible" status is inferred from records for nearby islands, relying largely on Bond (1956), Brudenell-Bruce (1975), and Connor and Loftin (1985).

Census counts were obtained by recording all birds seen and heard during 17 rapid walks (ca 3 km/h) covering 64 km along trails and roadsides during 30 May–21 July 1986 between 05:30 and 14:00 h (Table 1). Scrublands and woodlands, together with small patches of cultivation, account for about 90% of the total area surveyed, roughly proportional to the amount of area they cover on the island. Settlements account for about 5%, which is slightly more than their proportional area of the island, and mangroves, stands of casuarinas, and the edges of marshes or savannahs account for most of the remainder (ca 5%). Distances were estimated from Bahamas Government Maps (BLS series 318, scale 1:25,000).

Species-area and species-rainfall equations for calculating the predicted number of land bird species (excluding hawks) are $\log S = 0.970 + 0.160(\log A)$ and $S = -3.278 + 0.029(R)$, where S = species and A and R = island size and rainfall, respectively. The constants are from the equations for numbers of land birds on 11 Bahama Islands, not including Cat Island (Buden 1987).

All previous records are included for nonbreeding visitors; rare, scarce, and uncommon residents; and species whose status is uncertain. A species recorded on Cat Island for the first time is indicated by an asterisk.

SPECIES ACCOUNTS

Least Grebe (*Tachybaptus dominicus*).—Uncommon to fairly common resident. Usually seen at freshwater ponds with dense, emergent, weedy vegetation; occasionally on salt ponds. Breeding.—A half-grown young in a temporary freshwater pond, 3 km east of Smith Bay, 7 July 1986 (DWB); a nest with 4 eggs at a freshwater pond, 1 km north of Sandy Point, 8 July 1986 (DWB); an abandoned nest with 1 egg at a dried-out "saw grass pond," 0.5 km south of Gambier Lake, 23 July 1986 (DWB); a half-grown young collected 1 December 1963 (Paulson 1966).

White-tailed Tropic-bird (*Phaethon lepturus*).*—Status uncertain; possibly a summer visitor breeding in coastal cliffs and ledges. Three were seen off the highest cliffs between Port Howe and Columbus Point, 3 July 1986 (DWB), and one on the eastern coast opposite Knowles, 11 August 1982 (JPR and SFB).

Brown Pelican (*Pelecanus occidentalis*).*—Nonbreeding visitor. One was seen feeding close to shore near Flamingo Point, 12 July 1986 (DWB), and another seen at Hawks Nest Creek, August 1986 (C. Bostock and A. Chisholm).

Double-crested Cormorant (*Phalacrocorax auritus*) and Olivaceous Cormorant (*P. olivaceus*).—The status of these two species can not be assessed properly at this time because of insufficient data and records that pose more questions than they answer. The first mention of cormorants on Cat was by W. W. Worthington (in Todd and Worthington 1911) who included without comment "? Cat Island" among his locality records for *Phalacrocorax vigua* (=*olivaceus*). Bond (1956) reported *P. auritus* from "Cat Island (?)" probably inadvertently as the three previous editions of his check-list all mention a doubtful observation of *P. olivaceus* on Cat (presumably referring to Worthington's record), and none mentions *P. auritus* there. Later, sightings by J. R. Miller during the 1970s led Bond (1980) to suggest there was probably a colony of *P. olivaceus* on Cat Island. Miller (in litt.) recorded nests of *P. olivaceus* in December 1976 and on 15 December 1978.

I saw cormorants frequently at salt ponds during May–July 1986—maximum 85 together, Gambier Lake, 26 June. They were wary and generally did not allow close approach, but many of those observed through field glasses clearly showed the white facial border characteristic of *P. olivaceus*. The only specimens are bones of three individuals I found as partial skeletons on the shore of Gambier Lake, 26 June 1986. Storrs Olson (in litt.) considered two of them *P. auritus floridanus* and tentatively

assigned the other to an undescribed, diminutive subspecies of *P. auritus* known elsewhere only from San Salvador (see also Bond 1986). A resident of Zonicle Hill told me cormorants nested on islands in White Pond, usually beginning in August. I saw several cormorants (no nests) at the pond in July 1986, but was unable to visit the islands.

Magnificent Frigatebird (*Fregata magnificens*).—Nonbreeding visitor. Seen soaring high and offshore occasionally during June–July 1986 (DWB), and recorded during January and April 1908 (Todd and Worthington 1911) and on 9 July 1903 (Riley 1905). Widespread in the Bahamas generally, breeding on remote cays (Brudenell-Bruce 1975).

Great Blue Heron (*Ardea herodias*).*—Probably a nonbreeding visitor. Only four records: one seen in a tidal creek at Port Howe, 1 June 1986, another at Gambier Lake, 26 June 1986 (DWB); one seen at Tea Bay ponds, May 1982 (JPR and SFB); a skull and several limb bones collected at a "saw grass pond," 0.5 km south of Gambier Lake, 23 July 1986 (DWB).

Great Egret (*Casmerodius albus*).*—Status uncertain; possibly a rare breeder. No more than five seen during 23 May–28 July 1986 (DWB).

Snowy Egret (*Egretta thula*).*—Status uncertain; possibly a rare breeder. One seen at a salt pond south of Smokey Point, 12 June 1986 (DWB), another at Tea Bay ponds, 28 April 1982 (JPR and SFB).

Little Blue Heron (*Egretta caerulea*).*—Status uncertain; possibly a rare breeder. One immature seen in a tidal creek at New Bight, 23 May 1986 (DWB); one seen in a salt marsh at Smith Bay, 12 August 1982 (JPR and SFB).

Tricolored Heron (*Egretta tricolor*).*—Fairly common resident. Usually seen at salt ponds and tidal creeks. Breeding.—Colony, ca 50 adults and fledged young, 10–15 flightless young, many old nests, and 10 with 1–3 (mainly 2) eggs each, island at northern end of Gambier Lake, 26 June 1986 (DWB).

Reddish Egret (*Egretta rufescens*).*—Scarce summer visitor or resident. No more than five or six seen during June and July 1986, all of them white phase (DWB). Breeding.—A nest with 3 eggs, island at northern end of Gambier Lake, 26 June 1986 (DWB).

Cattle Egret (*Bubulcus ibis*).—Status uncertain; possibly breeding. Two seen during 27 November–2 December 1963 (Paulson 1966)—the first records; 2 seen, Alligator Point, 11 May 1981 (AS); 3 seen near airstrip at Arthur's Town, 11 June 1986, and 1 near Smith Bay, 4 July 1986 (DWB).

Green-backed Heron (*Butorides striatus*).*—Common resident and the most numerous heron. Found in all aquatic habitats and occasionally seen in scrublands far from water. Breeding (all records are 1986 [DWB]).—

Colony, 5 nests occupied by adults, salt pond north of Warren's Harbour, 28 May; a nest with 1 egg, mangrove flats at Fernandez Creek, 6 June; 4 nests (3 with 3 downy young each, 1 with 2 eggs), island at southern end of salt pond, north of Smokey Point, 12 June; colony, at least 6 pairs, some nests deep in patches of cactus (*Opuntia* sp.), eggs and young, island at northern end of Gambier Lake, 22 June; a nest with 3 eggs and another with 2, Guana Cay, off Port Howe, 3 July; 6 nests (2 with 2 eggs, 1 with 3 eggs, 1 with 1 egg and 2 nestlings, 1 with 1 nestling, 1 with 3 nestlings), island in Flamingo Pond, just west of Flamingo Point, 12 July. Most of the nests I saw were 1–3 m high in buttonwood trees (*Conocarpus erecta*), and most were over water.

Yellow-crowned Night-Heron (*Nycticorax violaceus*).*—Uncommon to fairly common resident; breeding is undocumented. Found mainly in aquatic habitats but seen also on roadsides and in cultivated areas (especially at night) and in scrublands and woodlands throughout. Approximately one fourth of those I saw during May–July 1986 were immatures.

Glossy Ibis (*Plegadis falcinellus*).*—Nonbreeding visitor. One seen at a salt marsh at Smith Bay, 12 and 23 August 1982 (JPR and SFB). There are few records for the Bahamas generally, though Brudenell-Bruce (1975) considers it an "uncommon passage migrant and vagrant" of regular occurrence on New Providence, and Connor and Loftin (1985) consider it a "sporadic visitor" on Eleuthera during autumn, winter, and spring.

Greater Flamingo (*Phoenicopterus ruber*).—Nonbreeding visitor. One photographed, 21–22 December 1976 (Miller in litt., Bond 1978).

West Indian Whistling-Duck (*Dendrocygna arborea*).*—Uncommon to fairly common resident, but breeding is undocumented. I saw and heard *D. arborea* in the southern half of Cat Island at freshwater ponds, in cultivated areas, and in flight regularly at night during May–July 1986. A pair seen on a rain-flooded trail 1.5 km east of McQueens during midafternoon, 19 June, is my only daytime record. One female with slightly enlarged follicles was collected (DWB) at a temporary freshwater pond 3 km east of Smith Bay, 22 June, and two individuals were hit by a car near New Bight, mid-June, but neither was collected (F. Major, pers. comm.). Villagers throughout the island consider *D. arborea* a permanent resident and an agricultural pest that feeds on corn and other crops.

White-cheeked Pintail (*Anas bahamensis*).*—Uncommon to fairly common resident at ponds and lakes throughout—maximum 10 together at McKinney Pond, 19 August 1982 (JPR and SFB). Breeding is undocumented, though many I saw during May–July 1986 were paired. Three "pairs" seen at Tea Bay ponds in December 1982 (JPR and SFB) are the only winter records.

Ruddy Duck (*Oxyura jamaicensis*).*—Status uncertain; possibly a rare

breeder. The four I saw at White Pond on 1 July 1986 are the only records. *O. jamaicensis* is an "uncommon permanent resident" and documented breeder on Eleuthera (Connor and Loftin 1985) and has been recorded elsewhere in the Bahamas previously only on New Providence, San Salvador, and Great Inagua (Brudenell-Bruce 1975).

Osprey (*Pandion haliaetus*).—Rare resident. A "pair" was seen at Flamingo Point, 17 May 1986, but no nest was found (AS). One example of the "West Indian subspecies," *P. h. ridgwayi,* was seen 27 May 1986, and one (possibly same bird) was seen 18 June 1986, both 1.5 km north of Fine Bay (DWB). Worthington (in Todd and Worthington 1911) recorded a *P. h. ridgwayi* seen at The Bight (=New Bight) 26 January 1909. Breeding.—A nest on a small cay at the entrance to Hawks Nest Creek contained eggs in 1978, but it has not been used in recent years (PM). I was told there were other nests on the coast between Hawks Nest Creek and Port Howe, but I found none. The darker headed, "continental race," *P. h. carolinensis* occurs widely in the Bahamas and the Antilles in winter and in passage (Bond 1956, Santana and Temple 1987) and may be expected to occur on Cat Island at times.

American Kestrel (*Falco sparverius*).—Uncommon resident (*F. s. sparveroides*) and a nonbreeding visitor (*F. s. sparverius*). The residents are most numerous in coconut (*Cocos*) groves in and near settlements. Breeding.—Several territorial birds (all very vocal, some swooping in attack) apparently were nesting in the crowns of coconut trees in Port Howe, Old Bight, New Bight, and Arthur's Town during May–July 1986 (DWB). I collected one *F. s. sparveroides* on 24 May 1986. This and all other kestrels I saw had snowy-white breasts characteristic of the pale phase of the "Cuban subspecies," which was reported on Cat Island first by Bond (1980) who based his remarks on sight records by J. R. Miller. Kestrels have been known as residents in the Bahamas only since 1960 (Schwartz and Klinikowski 1963), and Eleuthera is the northernmost record for *F. s. sparveroides* (see Bond 1986). Examples of the nominate race occur in the Bahamas in winter (Bond 1956); Paulson (1966) recorded the only one seen on Cat Island.

Clapper Rail (*Rallus longirostris*).—Probably a fairly common resident in mangrove swamps throughout. Heard calling from mangroves "on several occasions" during 27 November–2 December 1963 (Paulson 1966), and heard calling in the vicinity of tidal creeks regularly during May–July 1986 (DWB). No sightings and no other records.

Purple Gallinule (*Porphyrula martinica*).*—Probably a nonbreeding visitor. One collected dead (flattened) on the road between Fernandez Bay and New Bight, 24 July 1986 (DWB).

Common Moorhen (*Gallinula chloropus*).*—Scarce resident. Usually

seen in freshwater or slightly brackish ponds. Breeding.—Four half-grown young seen at a pond at the northern end of Tea Bay, 5 July 1986 (DWB).

American Coot (*Fulica americana*).*—Probably a fairly common nonbreeding visitor at ponds and lakes during winter, and possibly resident in small numbers. A flock of 15 was seen at the Tea Bay ponds in December 1982 (JPR and SFB). Local villagers told me coots were much more numerous in winter than summer. I saw only seven at three different localities in May and June 1986, and none in July.

Black-bellied Plover (*Pluvialis squatarola*).*—Nonbreeding visitor. Seen on beaches and tidal flats occasionally during May–July 1986 (DWB) and in August 1982 (JPR and SFB).

Wilson's Plover (*Charadrius wilsonia*).*—Probably a fairly common summer visitor, and possibly resident in small numbers. Usually seen on beaches and tidal flats and at shallow salt ponds. Recorded May–July 1986 (DWB) and August 1982 (JPR and SFB). Breeding.—Two downy young on a gravel causeway at Fernandez Creek, 18 June 1986, and two others on a sandy beach at Fine Bay, 21 June 1986 (DWB). There are no winter records of this plover for Cat Island, but Brudenell-Bruce (1975) considers it a "fairly common summer visitor" and a "rare resident or winter visitor" on New Providence, and Connor and Loftin (1985) state it is more common in summer than winter on Eleuthera.

Semipalmated Plover (*Charadrius semipalmatus*).*—Nonbreeding visitor. Two seen at Flamingo Pond, 18 May 1986 (AS), and five together at Tea Bay ponds, 15 August 1982 (JPR and SFB).

Killdeer (*Charadrius vociferus*).*—Uncommon to fairly common and probably resident. Observed in sparsely vegetated wet areas, including roadside puddles and rain-flooded yards during June–July 1986 (DWB). One that I collected (19 June) from among six on a beach at McQueens is a female *C. v. ternominatus* that had enlarged follicles. One seen on 9 July 1903 (Riley 1905), and one on 10 August 1982 (JPR and SFB) probably also were examples of the resident "West Indian subspecies." The nominate race may occur in winter and in passage, but I consider Worthington's sight record (in Todd and Worthington 1911) inconclusive.

American Oystercatcher (*Haematopus palliatus*).*—Probably an uncommon resident, but no winter records and breeding is undocumented. Pairs and single birds were seen on beaches (mainly at rocky headlands) regularly during May–July 1986 (DWB), and one was seen at Fernandez Creek, 14 August 1982 (JPR and SFB).

Black-necked Stilt (*Himantopus mexicanus*).*—Common summer visitor. Usually seen at salt ponds and in open areas in mangrove swamps. Breeding.—Eight nests (7 with 4 eggs, 1 with 2 eggs), 22 April 1984 (PM and MM), and 3 nests (2 with 4 eggs, 1 with 2 eggs) along with several

flightless young, 28 May 1986 (DWB), all at a pond north of Warren's Harbour; "4 pairs nesting," Tea Bay ponds, 1 May 1982 (JPR and SFB).

Greater Yellowlegs (*Tringa melanoleuca*).*—Nonbreeding visitor. Usually seen at ponds and tidal flats. Three were seen on 12 June, two on 19 June, two on 1 July, and one on 14 July, all 1986 and at different localities (DWB); one seen 12 August, another on 19 August 1982 (JPR and SFB).

Lesser Yellowlegs (*Tringa flavipes*).*—Nonbreeding visitor. Usually seen at ponds and tidal flats. Six were seen at Tea Bay ponds, and 2 others at Smith Bay, 14 July 1986 (DWB); recorded also on 2 May 1982 (JPR and SFB).

Willet (*Catoptrophorus semipalmatus*).*—Fairly common and probably resident, but no winter records and breeding is undocumented. Often seen at salt ponds and tidal flats, and occasionally on sandy and rocky beaches. All records are May–July 1986 (DWB) and August 1982 (JPR and SFB). Brudenell-Bruce (1975) considers it a "common resident" on most Bahama Islands, and Connor and Loftin (1985) state it is an "uncommon permanent resident" on Eleuthera.

Spotted Sandpiper (*Actitis macularia*).*—Nonbreeding visitor. Single birds seen 24 May, 14 July, and 18 July 1986 (DWB); "common at pond margins" in August 1982 (JPR and SFB).

Ruddy Turnstone (*Arenaria interpres*).*—Nonbreeding visitor. Seen frequently in small flocks of 5–10 on sandy and rocky beaches during May–July 1986 (DWB), and recorded in August 1982 (JPR and SFB). Presumably more numerous in winter, but no records.

Least Sandpiper (*Calidris minutilla*).*—Nonbreeding visitor. Five seen at Tea Bay ponds, 15 August 1982 (JPR and SFB).

Pectoral Sandpiper (*Calidris melanotus*).*—Nonbreeding visitor. An unspecified number seen at Tea Bay ponds, 11 August 1982 (JPR and SFB).

Short-billed Dowitcher (*Limnodromus griseus*).—Nonbreeding visitor. Sight records only: "large flock," Bennett's Harbour, 11 January 1957 (Bond 1957); one at Gambier Lake, 24 July 1986 (DWB); "dowitchers" (presumably *L. griseus*), Fernandez Creek, 14 August 1982, and at McKinney Pond, 19 August 1982 (JPR and SFB).

Laughing Gull (*Larus atricilla*).—Common to very common resident. Frequently seen on beaches and at salt ponds. Breeding.—Colony, ca 200 adults and 30 flightless young, island at northern end of Gambier Lake, 26 June 1986 (DWB).

Black-legged Kittiwake (*Rissa tridactyla*).—I consider the only record of two seen on 14 February 1984 (Norton 1984) in need of confirmation.

Gull-billed Tern (*Sterna nilotica*).*—Common to very common summer visitor. Usually seen at salt ponds and less frequently along the coast.

Breeding.—Colony, 75–100 adults, 25 nests (8 with 2 eggs, 5 with 3 eggs, 5 with 1 egg, 3 with 1 egg and 1 nestling, 1 with 1 egg and 2 nestlings, 1 with 2 eggs and 1 nestling, 1 with 2 nestlings, 1 with 3 nestlings), all on mud islands at the northern end of a salt pond north of Smokey Point, 11 June 1986 (ca 100 adults and recently fledged young, plus 5 nests with 1–3 eggs each and another with 1 egg and 1 nestling, same colony, 11 July 1986) (DWB); colony, ca 25 adults, 12 nests (5 with 2 eggs, 3 with 3 eggs, 3 with 1 egg, 1 with 2 eggs and 1 nestling), Brine Pond, east of New Bight, 16 June 1986 (DWB); colony, ca 50 adults, 13 downy young, 17 eggs, island at northern end of Gambier Lake, 26 June 1986 (DWB); ca 20 adults and 1 nest with 1 egg, Red Pond, north of Bain Town, 1 July 1986 (DWB); adult feeding a juvenile at Tea Bay ponds, 7–10 August 1982 (JPR and SFB).

Royal Tern (*Sterna maxima*).*—Uncommon generally and probably resident, but no winter records. Single birds and groups of 2–15 seen occasionally on beaches and tidal flats and at salt ponds during May–July 1986 (DWB). Breeding.—Colony, ca 100 adults, 50 downy young, and 10 nest "scrapes" with 1 egg each, island at northern end of Gambier Lake, 26 June 1986 (DWB).

Roseate Tern (*Sterna dougallii*).*—Probably a scarce summer visitor. Breeding.—Three pairs with 1 egg each, East Fernandez Cay, Fernandez Bay, 15 June 1986 (DWB); several individuals were seen at Flamingo Pond, 12 July 1986 (DWB).

Least Tern (*Sterna albifrons*).*—Fairly common summer visitor. Most numerous at salt ponds. Breeding (all records are 1986 [DWB]).—Colony, 15–20 adults, 6 clutches (4 with 2 eggs, 2 with 1 egg and 1 downy young), on flat rocks at southern end of salt pond north of Smokey Point, 11 June; pair copulating on sandbar, entrance to Bonefish Creek, 15 June; colony, 15–20 adults, 2 clutches (1 with 3 eggs, 1 with 1 egg), on flat rocks at northern end of Gambier Lake, 26 June.

Bridled Tern (*Sterna anaethetus*).—Common summer visitor. Usually seen in small colonies on the offshore cays, but seldom occurring on the "mainland." Breeding.—Twelve adults, 3 eggs, and 1 nestling on an unnamed cay 300 m offshore, Fernandez Bay, 15 June 1986 (DWB); 20–30 adults, 9 eggs, and 6 nestlings, East and West Fernandez cays, 15 June 1986 (DWB); ca 50 adults, 2 eggs, Guana Cay, off Port Howe, 3 July 1986 (DWB); "nesting," Port Howe Rock (=Guana Cay) (Sprunt 1984). All the clutches I found were comprised of one egg or nestling each, and they were on bare rock or pockets of sandy soil on ledges and cliffs.

Sooty Tern (*Sterna fuscata*).*—Probably a nonbreeding visitor, but nesting in large numbers in the Little San Salvador cays, ca 10 km east of Orange Creek (see Sprunt 1984). The only record for Cat Island is a

moribund individual I collected on a sandy beach north of Warren's Harbour, 30 June 1986.

Brown Noddy (*Anous stolidus*).*—Status uncertain. Possibly a summer visitor breeding on outlying cays. I saw ca 75 on Guana Cay and 10–15 on ledges at Columbus Point, 3 July 1986, but no evidence of nesting.

Rock Dove (*Columba livia*).*—Introduced. Uncommon and seen only in the settlements during May–July 1986 (DWB).

White-crowned Pigeon (*Columba leucocephala*).—Common to very common resident; more numerous in summer than in winter. Usually seen in coastal woodlands and mangrove swamps. Breeding (all records are 1986 [DWB]).—Two nests (1 with 3 eggs, 1 with 2 eggs), 6 June, and another with 2 eggs, 15 June, Fernandez Creek; a nest with 1 egg, East Fernandez Cay, Fernandez Bay, 15 June; a nest with 2 eggs, Bonefish Creek, 15 June; a nest with 2 eggs, Guana Cay, 3 July; many probable breeders heard calling and seen flying to and from islands at White Pond, north of Zonicle Hill, 1 July.

Zenaida Dove (*Zenaida aurita*).—Fairly common resident. Most numerous in cultivated areas. Breeding.—Eight nests with 2 eggs each, 29 May–8 July 1986, and 1 with 1 egg and another with 2 nestlings, 16 June 1986 (DWB). One of the nests was a grass-lined depression on the ground. The nine others were shallow bowls of twigs lined sparsely with leaves and were 1–4 m high in bushes and trees.

Mourning Dove (*Zenaida macroura*).—Status uncertain. Possibly a nonbreeding visitor or rare resident or both. Three sight records of single birds: during 27 November–2 December 1963 (Paulson 1966); Bennett's Harbour, 14 June 1986 (DWB); Old Bight, 13 August 1982 (JPR and SFB). That I saw only one during 23 May–28 July 1986 suggests nonbreeding visitor status only, but *Z. macroura* is widespread in the Bahamas and has been recorded breeding at least on New Providence (Bonhote 1903, Brudenell-Bruce 1975). Connor and Loftin (1985) consider it a "common permanent resident" on Eleuthera.

Common Ground-Dove (*Columbina passerina*).—Common resident. Most numerous in cultivated areas and along roadsides. Breeding.—Eight nests (4 with 2 eggs, 4 with 1 egg), 6 June–9 July 1986 (DWB).

Key West Quail-Dove (*Geotrygon chrysia*).*—Scarce resident. I saw no more than eight *G. chrysia* during 23 May–28 July 1986. All were in xeric woodlands and at three different localities—3 km southeast of Smith Bay, at Fernandez Bay, and between Port Howe and Gambier Lake.

Mangrove Cuckoo (*Coccyzus minor*).—Fairly common resident, but breeding is undocumented. Most numerous in scrublands and dense woodlands, and more often heard than seen.

Smooth-billed Ani (*Crotophaga ani*).*—Fairly common resident. Usu-

ally seen in scrublands, often in groups of 2–15. Breeding.—A pair at a nest of sticks and twigs, ca 6 m high in a dead tree between Tea Bay and Knowles, 14 July 1986 (DWB).

Common Barn-Owl (*Tyto alba*).*—Status uncertain, but probably a rare resident. One was heard calling and seen flying shortly after sunset 2.5 km east of Smith Bay, 20 June 1986 (DWB), and another was hit by a car at night in 1980 (F. Major, pers. comm.). In view of the availability of apparently suitable breeding sites (many caves and sinkholes) and food (rats, mice, and small birds), the scarcity of *T. alba* on Cat Island is unexpected. It is a fairly common resident on many Bahama Islands, including the Caicos Bank.

Burrowing Owl (*Athene cunicularia*).—Uncommon to fairly common resident. Usually seen in cultivated fields and open areas generally; active during day and night. Most numerous in the fields between Smith Bay and Old Bight—maximum six together east of Old Bight, 28 May 1986, and east of Smith Bay, 1 June 1986 (DWB). Breeding is not confirmed, but I saw four individuals near the entrance to a burrow in sandy soil in a grassy and weedy swale 200 m from the beach at the northern end of New Bight, 23 May 1986.

Antillean Nighthawk (*Chordeiles gundlachii*).*—Common summer visitor. Usually seen hawking for insects at dawn and dusk, mainly over roadways and coastal scrub. Maximum 15 together, Arthur's Town, 10 June 1986 (DWB). Breeding (all records are 1986 [DWB]).—Five eggs (28 May, 26 June, 3, 21, and 24 July) and 4 nestlings (21 and 30 June, 1 and 16 July). All nine "nests" were on the ground in sparsely vegetated areas, mainly beaches and the open shorelines of salt ponds.

Bahama Woodstar (*Calliphlox evelynae*).—Fairly common resident in terrestrial habitats throughout. Breeding.—A nest with 2 eggs, 20 June 1986 (DWB).

Belted Kingfisher (*Ceryle alcyon*).*—Nonbreeding visitor. Occurs regularly in winter (PM and MM), and one seen at Tea Bay ponds, 10 August 1982 (JPR and SFB).

Greater Antillean Pewee (*Contopus caribaeus*).—Uncommon resident. Seen and heard calling from the tops of tall trees in scrublands and woodlands regularly during June and July 1986, and one specimen (*C. c. bahamensis*) collected 14 June 1986 (DWB). The only other record is one collected 28 November 1963 by D. R. Paulson who saw no others during 27 November–2 December (Paulson 1966).

Eastern Kingbird (*Tyrannus tyrannus*).—Nonbreeding visitor. A sight record for 4 July by R. W. Hanlon (Bond 1959).

Gray Kingbird (*Tyrannus dominicensis*).—Common to very common summer visitor. Most numerous in settlements and coastal stands of

casuarinas. Frequently heard calling from the tops of tall trees and on telephone lines, and often beginning an hour or more before sunrise. Breeding.—Eight active nests (1 with 3 eggs on 16 June, another with 3 nestlings on 11 July), most of the 3–15 m up in trees (mainly casuarinas), all 7 June–23 July 1986 (DWB).

Barn Swallow (*Hirundo rustica*).—Nonbreeding visitor. No more than a few seen during 27 November–2 December 1963 (Paulson 1966), and a flock of 10–15 seen at Sandy Point, 17 May 1986 (AS).

Hermit Thrush (*Catharus guttatus*).—Nonbreeding visitor. One seen 18 December 1976 (Miller in litt., Bond 1978).

Red-legged Thrush (*Turdus plumbeus*).—Uncommon to fairly common resident. Usually seen in woodlands and dense scrublands, occasionally in trees in open, cultivated areas and in settlements. Many of those I saw during May–July 1986 were singing from exposed perches and several were feeding on both fallen and attached figs (*Ficus*). I collected two *T. p. plumbeus* on 3 March 1968, and two others on 28 May and 8 July 1986. The Red-legged Thrush has been recorded previously on Cat Island only by Riley (1905) who said it was "found sparingly."

Northern Mockingbird (*Mimus polyglottos*).—Scarce to uncommon resident and rarely seen outside the settlements. First recorded on Cat Island by R. W. Hanlon, presumably in 1958 (see Bond 1959). The only other records are a few individuals seen during 27 November–2 December 1963 (Paulson 1966), 10–15 seen during May–July 1986 (DWB), and several seen in August 1982 (JPR and SFB). Breeding.—A nest with 4 eggs 2 m high in a thorny tree in a vacant yard, Industrious Hill, 14 July 1986 (DWB).

Bahama Mockingbird (*Mimus gundlachii*).—Very common resident in terrestrial habitats throughout; the most abundant land bird. Breeding (all records are 1986 [DWB]).—Three nests under construction, 30 May, 15 June, and 20 June; 3 nests with 2 eggs each, 26 June, 13 July, and 20 July; 2 nests with 3 eggs, 2 and 11 July; 1 nest with 1 egg and 1 nestling, 13 June; 1 nest with 2 nestlings, 7 July; 1 nest with 3 nestlings, 14 July. Two of the 11 active nests I found were on the ground; the nine others were 1–3 m high in trees and bushes. Ten were constructed largely of sticks and lined sparsely with thinner twigs and occasionally grasses. One was made entirely of grasses and was on the ground near the edge of the tarmac on the New Bight airstrip. The eggs were pale, bluish-gray or bluish-white with dark brown spots and streaks, the markings being especially dense at the larger end. The mouth-linings of two nestlings were vivid yellow.

Pearly-eyed Thrasher (*Margarops fuscatus*).—Nonbreeding visitor. The only record is one bird seen in late November 1963 (Paulson 1966).

Although *M. fuscatus* has been recorded occasionally on the Great Bahama Bank (Eleuthera, Great Exuma, Cat, and Long islands), it apparently is not established there (see Paulson 1966, Bond 1977, 1978, 1980). It is common in the southern Bahamas and breeds as far north as San Salvador (Paulson 1966, Miller 1978).

Water Pipit (*Anthus spinoletta*).—Nonbreeding visitor. One photographed 23 December 1976 (Miller, in litt., Bond 1977).

European Starling (*Sturnus vulgaris*).—Probably a nonbreeding visitor. Ten seen 29 November 1963 (Paulson 1966). Becoming increasingly more numerous in the northern Bahamas in recent years, mainly during autumn and winter (Brudenell-Bruce 1975, Connor and Loftin 1985), but no evidence of breeding.

White-eyed Vireo (*Vireo griseus*).*—Nonbreeding visitor. One seen at Tea Bay, April 1982 (JPR and SFB).

Thick-billed Vireo (*Vireo crassirostris*).—Very common resident. Most numerous in woodlands and dense scrublands. Breeding.—Two nests with 2 eggs, 7 and 14 June 1986, and 2 others with 3 eggs, 31 May and 13 July 1986 (DWB).

Black-whiskered Vireo (*Vireo altiloquus*).*—Uncommon summer visitor. Most numerous in woodlands, and usually high in the canopy. Breeding not confirmed, but many I saw during May–July 1986 were paired.

Blue-winged Warbler (*Vermivora pinus*).—Nonbreeding visitor. One collected 28 November 1963 (Paulson 1966). The lack of winter records of this and other warbler species should not suggest that many are not common during that season.

Yellow Warbler (*Dendroica petechia*).*—Uncommon and presumably resident. Occurring in mangrove swamps and immediately adjacent scrub. Seen and heard singing during June and July 1986 (DWB) and August 1982 (JPR and SFB). Breeding (all records are 1986 [DWB]).—Two nests, both ca 1 m high in the tops of small black mangroves (*Avicennia nitida*): 1 with 3 eggs (Fernandez Creek, 6 June), the other empty (1 km east of McQueens, 16 June); 2 or 3 recently fledged young soliciting food from an adult at Old Bight, 20 June. No specimens were collected, but all records presumably are the resident "Cuban-Bahaman subspecies," *D. p. gundlachii,* which occurs also in the Florida Keys.

Magnolia Warbler (*Dendroica magnolia*).—Nonbreeding visitor. Two seen (one collected) during 27 November–2 December 1963 (Paulson 1966).

Yellow-throated Warbler (*Dendroica dominica*).*—Nonbreeding visitor. One seen at Fernandez Bay, 16 August (JPR and SFB).

Kirtland's Warbler (*Dendroica kirtlandii*).—Nonbreeding visitor. One specimen (Academy of Natural Sciences, Philadelphia, number 48134)

collected 20 November 1890 by J. Percy Moore (M. Robbins, in litt., see also Bond 1951).

Prairie Warbler (*Dendroica discolor*).—Nonbreeding visitor. Eleven collected 11 March 1886 (Ridgway 1891); two collected in November 1890 by J. Percy Moore.

Palm Warbler (*Dendroica palmarum*).—Nonbreeding visitor. Eight collected 11 March 1886 (Ridgway 1891) and one or more seen on 26 January 1909 (Todd and Worthington 1911).

American Redstart (*Setophaga ruticilla*).—Nonbreeding visitor. One seen 4 July by R. W. Hanlon (Bond 1959).

Worm-eating Warbler (*Helmitheros vermivorus*).—Nonbreeding visitor. Two specimens collected by D. R. Paulson on 30 November and 1 December 1963 (see Paulson 1966).

Swainson's Warbler (*Limnothlypis swainsonii*).*—Nonbreeding visitor. One collected 3 March 1968 (DWB).

Ovenbird (*Seiurus aurocapillus*).—Nonbreeding visitor. One collected 11 March 1886 (Ridgway 1891).

Louisiana Waterthrush (*Seiurus motacilla*).—Nonbreeding visitor. One seen during late November 1963 (Paulson 1966), and another on 7 August 1982 (JPR and SFB); 1 collected (partially decomposed) 17 July 1986, and 2 seen (one collected) on 24 July 1986 (DWB). The Northern Waterthrush (*S. noveboracensis*) is more common than the Louisiana Waterthrush in the Bahamas generally (Bond 1956, Paulson 1966, Brudenell-Bruce 1975, Connor and Loftin 1985), but it is unrecorded on Cat Island.

Common Yellowthroat (*Geothlypis trichas*).—Nonbreeding visitor. One collected 11 March 1886 (Ridgway 1891).

Bahama Yellowthroat (*Geothlypis rostrata*).—Fairly common resident, but breeding is undocumented. Usually seen in woodlands and dense scrublands, and generally low (ground to 3 m high) in the vegetation. I found it most numerous between the settlements of Devil's Point and McQueens—10 seen and heard during a 2-h walk (09:00–11:00) covering 6.5 km on 19 June 1986. *G. rostrata* was recorded on Cat Island for the first time by Paulson (1966) who "observed from one to three individuals at almost every locality visited" during 27 November–2 December 1963; he collected 2 specimens. I collected 5 on 2 and 3 March 1968 and five others during May–July 1986. The Cat Island population belongs to the race *G. r. coryi*, which occurs elsewhere only on Eleuthera.

Hooded Warbler (*Wilsonia citrina*).—Nonbreeding visitor. One male seen 29 November 1963 (Paulson 1966).

Bananaquit (*Coereba flaveola*).—Common resident in terrestrial habitats throughout, but breeding is undocumented.

Stripe-headed Tanager (*Spindalis zena*).—Uncommon resident in ter-

restrial habitats throughout; breeding is undocumented. Nearly half of those I saw during May–July 1986 were in *Ficus* trees and feeding on the figs. Others were calling from exposed perches in cultivated areas and in the settlements. Two *S. z. zena* were collected on 28 November 1963 by D. R. Paulson, another in November 1890 by J. Percy Moore, and five on 11 March 1886 by the *Albatross* Expedition (Ridgway 1891). Worthington (in Todd and Worthington 1911) mentioned a sight record for 6 April 1909.

Indigo Bunting (*Passerina cyanea*).—Nonbreeding visitor. Two specimens collected 11 March 1886 (Ridgway 1891).

Black-faced Grassquit (*Tiaris bicolor*).—Common resident. Most numerous in casuarinas and in weedy areas, especially roadsides and farmlands. Breeding (all records are 14 June–23 July 1986 [DWB]).—Nine active nests, all 0.5–2 m high in bushes, 1 with 1 egg, 2 with 2 eggs, 2 with 3 eggs, 1 with 1 egg and 1 nestling, 1 with 2 nestlings, 2 with 3 nestlings.

Greater Antillean Bullfinch (*Loxigilla violacea*).—Very common resident, but breeding is undocumented. Most numerous in dense scrublands and not infrequently seen gleaning figs in settlements and woodlands (DWB).

Savannah Sparrow (*Passerculus sandwichensis*).—Nonbreeding visitor. One collected on 2 December 1963 by D. R. Paulson.

Snow Bunting (*Plectrophenax nivalis*).—Nonbreeding visitor. One collected 1 December 1963 (Paulson 1966).

DISCUSSION

Of the 97 species of birds known from Cat Island and immediately adjacent cays, at least 47 probably breed there; no species or subspecies is endemic. Excluding the introduced Rock Dove, 24 of the probable breeders are land birds (pigeons to passerines, plus 1 kestrel) (Table 1), 11 are shorebirds (charadriiforms), 4 are herons, 2 are ducks, and the remaining 5 (six, if 2 species of cormorants breed) include a grebe, cormorant, Osprey, and 2 rails. Others possibly breeding, but known only form very few records include 1 land bird (Mourning Dove) and 8 waterbirds (White-tailed Tropicbird, Great Egret, Snowy Egret, Little Blue Heron, Cattle Egret, Ruddy Duck, American Coot, Brown Noddy); all of them have been confirmed breeding on at least one island elsewhere in the Bahamas. The numbers of land birds (excluding hawks) predicted both from island size (24 species) and the available rainfall data (26 species) agree fairly with the 23 recorded (see Methods). The wetter islands in the Bahamas tend to have greater habitat diversity and a more luxuriant vegetation than the drier ones, and, together with the larger islands, more

bird species (Buden 1977). Along these gradients, Cat Island falls roughly in the middle.

Most of the indigenous, breeding land birds of Cat Island are widespread in all the terrestrial habitats. The Yellow Warbler, however, occurs only in the mangroves and immediately adjacent scrub, the Northern Mockingbird is rarely seen outside the settlements, and the Key West Quail-Dove apparently is confined to the woodlands. Habitat preferences are also pronounced in several other species including American Kestrel (coconut groves near settlements), Burrowing Owl (cultivated areas), Antillean Nighthawk (dry, sparsely vegetated areas), Gray Kingbird (casuarinas and settlements), and Black-faced Grassquit (casuarinas and weedy areas). The White-crowned Pigeon is most numerous in mangroves and woodlands, and the Zenaida Dove and Common Ground-Dove occur most frequently on roadsides and in cultivated areas.

Table 1 lists the indigenous land birds of Cat Island in decreasing order of abundance based on general field observations together with the results of 17 census counts. The counts probably underestimate population size, as some birds seen and heard were unidentified and others doubtless went undetected during the rather fast walks (ca 3 km/h). With few exceptions, however, the counts match well the scale of relative abundance based on general observations. The Gray Kingbird and Antillean Nighthawk both are more numerous than the 17 counts indicate, but the kingbird is abundant only near settlements and in stands of casuarinas, and the nighthawk is crepuscular and thus often overlooked during daytime surveys. The slightly higher count for the Greater Antillean Pewee among "uncommon species" is due to 5 individuals seen in 2 km between Greenwood and Port Howe on 2 July 1986. The absence of the Yellow Warbler in the counts probably is due to its preference for low mangroves in tidal creeks, which were poorly represented in the 17 surveys.

For the most part, the species of birds breeding on Cat Island are widespread in the Bahamas generally. The Bahama Yellowthroat and Red-legged Thrush, however, both fairly common in mesic woodlands and thickets in the northern Bahamas, do not breed in the southern Bahamas. The thrush has been recorded once on Great Inagua (Sprunt in Bond 1962), but apparently is not established there. Conditions in the southern part of the chain may be too xeric to support them; alternatively, they may not have reached the relatively small banks that comprise the southern Bahamas in sufficient numbers to colonize. The "Cuban-Bahaman race" of the American Kestrel, on the other hand, occurs only as far north as Eleuthera (see Bond 1986), but it is a recent arrival to the Bahamas (see species account) and has been expanding its range northward. The Pearly-eyed Thrasher is common in the southern Bahamas and has been

TABLE 1

INDIGENOUS, BREEDING LAND BIRDS OF CAT ISLAND, IN DECREASING ORDER OF ABUNDANCE BASED ON GENERAL OBSERVATIONS AND WITH THE NUMBER OF BIRDS SEEN AND HEARD/KM DURING 17 COUNTS COVERING 64 KM

Species	Abundance[a]	Birds/km
Bahama Mockingbird (*Mimus gundlachii*)	VC	5.8
Thick-billed Vireo (*Vireo crassirostris*)	VC	3.4
Greatern Antillean Bullfinch (*Loxigilla violacea*)	VC	2.8
White-crowned Pigeon (*Columba leucocephala*)	C–VC	2.1
Gray Kingbird (*Tyrannus dominicensis*)	C–VC	1.2
Black-faced Grassquit (*Tiaris bicolor*)	C	1.9
Bananaquit (*Coereba flaveola*)	C	1.6
Common Ground-Dove (*Columbina passerina*)	C	1.1
Antillean Nighthawk (*Chordeiles gundlachii*)	C	0.1
Bahama Yellowthroat (*Geothlypis rostrata*)	FC	0.7
Zenaida Dove (*Zenaida aurita*)	FC	0.6
Smooth-billed Ani (*Crotophaga ani*)	FC	0.5
Mangrove Cuckoo (*Coccyzus minor*)	FC	0.4
Bahama Woodstar (*Calliphlox evelynae*)	FC	0.4
Red-legged Thrush (*Turdus plumbeus*)	UC–FC	0.2
Burrowing Owl (*Athene cunicularia*)	UC–FC	0.1
Black-whiskered Vireo (*Vireo altiloquus*)	UC	0.1
Greatern Antillean Pewee (*Contopus caribaeus*)	UC	0.2
American Kestrel (*Falco sparverius*)	UC	0.1
Stripe-headed Tanager (*Spindalis zena*)	UC	0.1
Yellow Warbler (*Dendroica petechia*)	UC	0.0
Northern Mockingbird (*Mimus polyglottos*)	S–UC	0.0
Key West Quail-Dove (*Geotrygon chrysia*)	S	0.0
Common Barn-Owl (*Tyto alba*)	R	0.0

[a] VC = very common, C = common, FC = fairly common, UC = uncommon, S = scarce, R = rare; see Methods for additional explanation.

recorded once on Cat Island, but it is not known to be established anywhere on the Great Bank.

The absence of La Sagra's (formerly Stolid) Flycatcher (*Myiarchus sagrae*) and Blue-gray Gnatcatcher (*Polioptila caerulea*) and the rarity of the Common Barn-Owl are somewhat unexpected. All three are widespread in the archipelago, although the gnatcatcher is absent on many islands in the central Bahamas, and the distribution of the flycatcher is spotty in the southern Bahamas. A medium-sized tyrannid with a reddish-brown tail that I saw fleetingly and poorly in xeric woodlands between Port Howe and Gambier Lake on 2 July possibly was a La Sagra's Flycatcher.

Many of the birds on Cat Island breed during summer, but there are

insufficient data for further generalizations regarding breeding cycles. Paulson (1966) recorded a half-grown Least Grebe taken in December 1963, and P. and M. Mann (pers. comm.) reported an Osprey nest active in 1978 and Black-necked Stilts nesting in April 1984. J. Perran Ross and Sarah Fay Baird (in litt.) reported Black-necked Stilts nesting in May 1982 and a juvenile Gull-billed Tern being fed by an adult in August 1982. Miller (in litt.) reported Olivaceous Cormorants nesting in December 1976 and 1978. All other records of breeding are mine from summer 1986.

During 23 May–28 July, I found active nests, eggs, or young of 13 species of waterbirds and 12 species of land birds. Additionally, territorial American Kestrels probably had nests in the tops of coconut trees, and groups of up to six Burrowing Owls seen regularly at the same localities during the summer probably had nesting burrows nearby. The nests of Gray Kingbirds usually were at least 3–15 m high in trees (mainly casuarinas), and the one Smooth-billed Ani nest was 6 m high in a tree. Eleven species nested usually 0.5–4 m high in bushes and small trees, although some nests among those of the White-crowned Pigeon (1 of 6), Zenaida Dove (1 of 8), and Bahama Mockingbird (2 of 11) were on the ground. The eight other species that usually had nests low in bushes and trees were Tricolored Heron, Green-backed Heron, Common Ground-Dove, Bahama Woodstar, Northern Mockingbird, Thick-billed Vireo, Yellow Warbler, and Black-faced Grassquit. Ten species nested only on the ground. Five of them were terns (Gull-billed, Royal, Roseate, Least, Bridled), one was a land bird (Antillean Nighthawk), and the four others were Least Grebe, Reddish Egret, Black-necked Stilt, and Laughing Gull. Among the more common birds on Cat Island that I did not observe nesting were the Bananaquit and Greater Antillean Bullfinch.

In summary, roughly half of the 97 species of birds known from Cat Island breed there, and approximately half of these are land birds. Additional winter surveys doubtless will provide many more records of nonbreeding visitors, but few land birds are likely to be added to the list of breeding species as the number recorded is close to predicted values, and because the species composition is generally similar to that found on comparable, nearby islands. The status of many of the waterbirds is uncertain; eight are considered potential breeders. Most of the species seem to breed mainly in summer (May–August) and usually nest on the ground or only 2–3 m high in the vegetation.

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Cat Island turtle; F. Major, District Education Officer, Cat Island; P. and M. Mann, teachers at Old Bight High School during 1976–1986; and A. Sprunt, Research Director, National Audubon Society, who visited Cat Island in 1981 and 1986. I thank J. R. Miller for additional data supplementing his records published elsewhere; S. Olson for identifying bones of cormorants to subspecies; J. V. Remsen, Jr. for copies of pages of Schwartz's catalog covering Cat Island collections; and M. Robbins for a list of birds collected by J. P. Moore. M. H. Clench and A. Sprunt reviewed the manuscript and provided suggestions for its improvement. Permission to do field work and collect in the Bahamas was granted by the Bahamas Department of Agriculture and the Bahamas National Trust. Their cooperation and prompt attention to requests have been greatly appreciated.

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The North American Loon Fund (NALF) announces the availability of two grant programs for support of new or current research, management, or education projects that may yield useful information for Common Loon conservation in North America.

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Wilson Bull., 99(4), 1987, pp. 601–610

THE EFFECTS OF DISTANCE AND ISOLATION ON SONG-TYPE SHARING IN THE CAROLINA WREN

EUGENE S. MORTON[1]

ABSTRACT.—I describe the geographic distribution of song types in the Carolina Wren (*Thryothorus ludovicianus*) in continuous and discontinuous populations along the eastern shore of the Chesapeake Bay and adjacent islands. On average, individuals at the same site held 66% of their songs in common (range = 49.5–89.5%). At sites in continuous mainland populations, I found a negative linear correlation between the distance separating individuals and the percentage of songs shared. Wrens on isolated island sites shared less than 20% of their song types with individuals on the nearest mainland areas. Song sharing among males separated by 3 km of water was equivalent to that found in males separated by 145 km of continuous mainland habitat. Of the 309 song types in the total sample, 78% were restricted to one site. The percentage of songs shared among neighboring free-ranging wrens found in this study is compared to the percentage of undegraded songs learned by naive young males in a laboratory experiment. *Received 16 Feb. 1987, accepted 25 May 1987.*

Many recent studies of the functional significance of song sharing among neighboring male oscines focus on distance assessment as an important source of selection on the evolution of song types and song repertoires (McGregor and Krebs 1984; Morton 1982, 1986; Shy and Morton 1986), and on the song types learned by individual birds (Morton et al. 1986). In the Carolina Wren (*Thryothorus ludovicianus*), a male hearing a conspecific song uses degradation in the perceived song to assess its distance from the singer (Richards 1981, Wiley and Richards 1982, Shy and Morton 1986). This ranging of distance is possible only if the listener has the song type it perceives stored in its memory (i.e., it has an undegraded replica of what it hears) (Morton 1986, Shy and Morton 1986). Young males base their choice of songs to learn on the amount of degradation in songs they hear, at least in the laboratory (Morton et al. 1986). This finding supports Hansen's (1979) hypothesis that local acoustic environments, in conjunction with choice during song learning, act as a "filter" selecting song types adapted to local acoustic conditions. This preferential learning of relatively undegraded songs also would result in songs being shared by neighbors because of the close proximity of neighbors relative to other conspecific singers. Close proximity would result in less degradation in perceived songs and these would, therefore, be learned preferentially. This is supported by a field study showing that the ca 32 songs learned by each Carolina Wren (range = 17–42 [Chu 1979], 25–43 [Simp-

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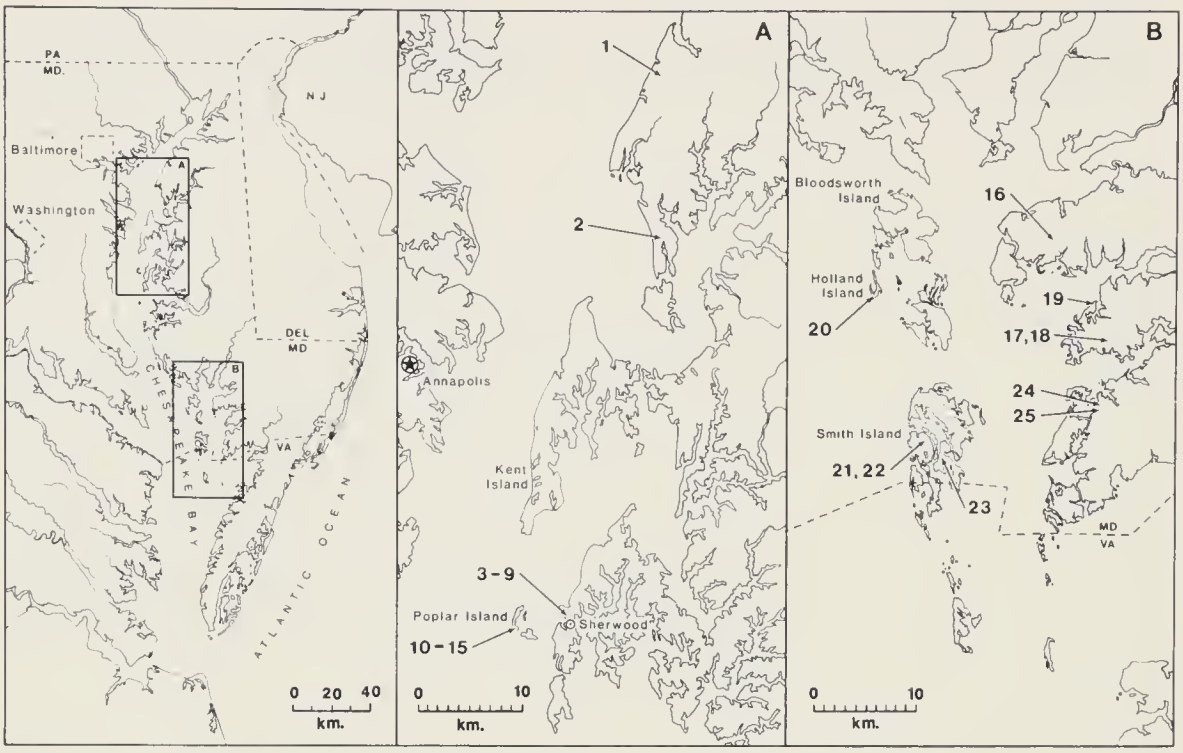

FIG. 1. Map of the Chesapeake Bay study area with enlargements (A and B) showing locations of the 25 male Carolina Wrens whose song types were analyzed.

son 1985]) are chiefly those that degrade less (when tape recordings are played and recorded 50 m away) in their native habitat than in foreign habitats (Gish and Morton 1981).

Although we can predict the basis upon which an individual learns particular song types, we know little about the larger distribution of song types in Carolina Wrens. Over how large an area does a particular song type occur? Are song types grouped geographically or is each distributed independently? Here we describe the effects of isolation, either by distance or water barriers, on the geographic distribution of Carolina Wren song types and on the extent to which they are shared by males separated to various degrees. This provides a base from which to compare naturally occurring song sharing with data from a laboratory experiment on the effects of degradation on songs learned (Morton et al. 1986).

STUDY AREA AND METHODS

The study was conducted at seven sites along a 145-km transect on the Eastern Shore of Maryland and four adjacent islands (Poplar, Smith [two adjacent islands], and Holland) in the Chesapeake Bay (Fig. 1). Carolina Wrens repeat an unvarying song type many times before switching to another song type (Kroodsma 1977). We call each continuous repetition of a song type a bout (="song series" of Borror 1956). We recorded bouts of song from 25 male wrens at 11 sites from March through August, using a Uher 4000 Report IC tape recorder (19.05 cm/sec recording speed) and Dan Gibson EPM model P-200 parabolic microphone.

Earlier, we determined that a minimum of 60 bouts is usually needed to guarantee that a complete repertoire has been recorded (Chu 1979). Many males, especially young ones (Simpson 1984), however, cycle through their repertoires in fewer than 60 bouts. For example, a captive male, recorded continuously for three days, reached asymptote after 45 bouts were recorded (his repertoire consisted of 27 song types). Thus, we feel that we obtained full repertoires for all of the birds for which we obtained 60 or more bouts (64% of sample), as well as most of the remaining birds sampled (number of bouts sampled per male ranged from 35 to 139 with a mean of 75).

Approximately 10 songs from each bout were recorded and analyzed. We recorded the songs of one individual at a time over one or more days. The birds were not banded, but previous work has shown that this species is sedentary and defends the same territory year-round (Morton and Shalter 1977). Morton (unpubl. data) found no territory changes among males in a color-banded population over three years (see also Simpson 1985, p. 794). Thus, our focus on one male on the same territory over a short period of time would adequately ensure that the same individual was recorded each day.

Spectrograms of songs from each male were made with a Kay Elemetrics Corp. Type 7029A sound spectrograph using the FL-1 circuit, 300 Hz "wideband" filter setting and the 80–8000 Hz analyzing range. The song consists of identical repeated syllables each composed of a variable number of elements (examples of spectrograms are found in Borror 1956, Richards 1981, Gish and Morton 1981). As the song is not complex, we were able to classify songs as the same or different based upon examination of spectrograms. When comparing one song with another the criteria used for assessing their similarity were (1) element-for-element matching, (2) approximate or exact correspondence in frequency (Hz), and (3) duration of a syllable (terms follow Gish and Morton 1981). Spectrograms of all songs and their classification are in Chu (1979). The following quantitative measures were taken for each song type: number of elements per syllable, highest and lowest frequency (kHz), syllable duration (msec), and intersyllable interval (msec). These measures were used to compare unusually widespread song types with those having a more limited distribution.

We first recorded the song repertoires of the entire wren population (6 males) on Poplar Island for comparison with wrens at the closest mainland site, a distance of 3 km. For this island-mainland comparison, we recorded 7 mainland males on adjacent territories along a 3-km transect perpendicular to the mainland to island axis. This protocol was repeated for comparisons with the two Smith Islands and Holland Island and their nearest mainlands. Only one or two wrens occurred on these islands, however, so we emphasize the Poplar Island-mainland comparison. In addition, song-type sharing was calculated within and among all sites.

Sharing is expressed as the average percentage of the song repertoire shared between two individuals. Thus if male 1 shares 60% of its song types with male 2 and male 2 shares 50% of its song types with male 1, they share an average of 55%. Site comparisons were based on similarity in composition of the pooled song types from any two localities.

Distances between recording sites were measured from a map as the shortest land distance for mainland to mainland comparisons. For island to mainland comparisons, the distance from the island to the nearest mainland was summed with the shortest land distance between this landfall and the mainland site of interest.

RESULTS

We recorded 1812 song bouts and identified 309 song types from the 25 males. The mean repertoire consisted of 29.0 ± 6.8 song types [SD] (range = 17–42). Using only birds for which 60 bouts or more were obtained (N = 16), the mean repertoire size was 32.4 song types (median =

TABLE 1

NUMBER OF SONG TYPES SHARED AMONG CAROLINA WRENS AT POPLAR ISLAND (6 MALES) AND THE CLOSEST MAINLAND (7 MALES)

Bird no.[a]	No. in population sharing song types[b]						Song types shared/total in repertoire	% shared
	2	3	4	5	6	7		
Poplar Island								
10	4	3	8	10	8		33/36	92
11	3	3	6	11	8		31/31	100
12	0	1	3	6	8		18/19	95
13	2	5	6	10	8		31/32	97
14	0	4	1	7	8		20/20	100
15	5	2	8	11	8		34/36	94
Mainland								
3	2	1	4	2	10	4	23/23	100
4	3	3	2	4	11	4	27/35	77
5	3	1	2	0	7	4	17/17	100
6	6	3	4	4	12	4	33/34	97
7	2	3	2	2	13	4	26/26	100
8	5	2	1	4	12	4	28/29	97
9	7	2	2	4	13	4	33/34	100

[a] Same number and location of the bird as in Fig. 1.
[b] For example, bird 10 had four songs shared with one other population member, three songs shared with two, etc.

32, range = 19–42). The mean repertoire size for birds for which less than 60 bouts were recorded (N = 9) was 23.0, which was also the median value (range = 17–29). These values are comparable to data from North Carolina (Simpson 1985).

The percentage of repertoires shared by males holding adjacent territories averaged 64.3% (males 3–9), 64.8% (males 17, 18), 64.2% (males 24, 25) for 3 mainland sites, and 68.9% (males 10–15) for Poplar Island. The extent of song sharing among males within two sites, Poplar Island and the mainland adjacent to Poplar Island, is given in Table 1. From 95–96% of the pooled song types for each site occur in the repertoires of two or more males at that site. Thus, while a group of males having contiguous territorial boundaries share about 64–69% on average of their repertoires of song types (range = 49.5–89.5%) in pairwise comparisons, the likelihood of a given song type occurring among at least two males in a small population of males at the same site (only some of which have contiguous territories) is much greater. Thus, immediate neighbors may share fewer song types than is possible, indicating a possible preference for learning some songs not the repertoire of contiguous neighbors (Morton et al. 1986).

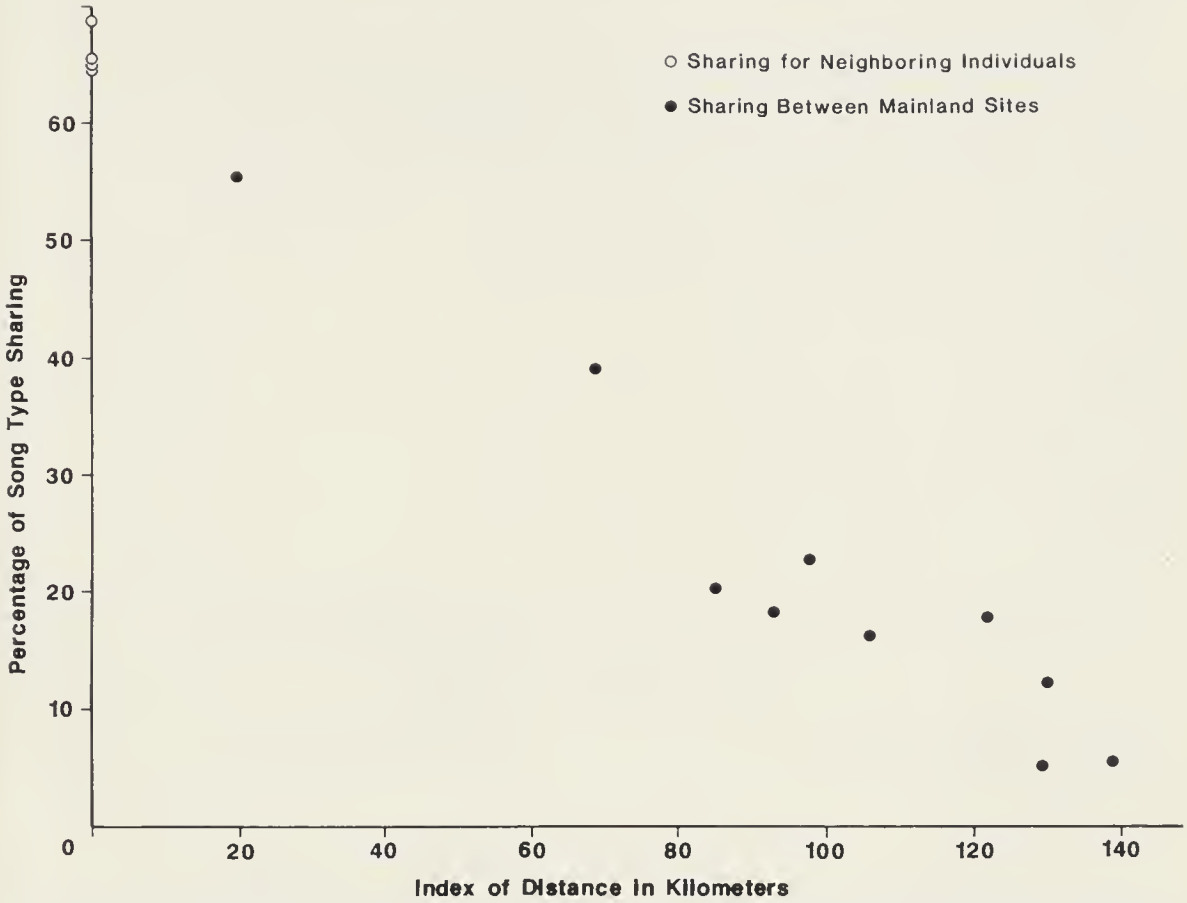

FIG. 2. Song sharing in percentage between neighboring individuals at the same site (open circles) and between mainland sites with no water barriers separating them (closed circles), as a function of distance separating them.

There was a highly significant negative correlation between distance and the percentage of song types shared ($r = -0.98$, $P < 0.001$) (Fig. 2). Removing males on adjacent territories (0 distance in Fig. 2) from the analysis still results in a highly significant negative correlation ($r = -0.95$, $P < 0.001$). In contrast, sites separated by water (island to mainland and island to island comparisons, $r = -0.21$ and $r = -0.04$, respectively, $P > 0.1$ for both) show no correlation with distance and percentage song sharing (Fig. 3).

The distribution of the 309 song types was highly skewed (Table 2); most (242, 78.3%) were found at only one site. Most (95%) of these unique song types were found in the repertoire of at least two birds at the site. Although there was no difference between wrens at the island and mainland sites in the uniqueness of their repertoires ($\chi^2 = 8.6$, df = 6, $P > 0.1$), it was our impression that island-inhabiting birds had more atypical songs. For example, the only song in our sample that was clearly mimicked (a Pine Warbler [*Dendroica pinus*]) was sung by two wrens on Poplar Island.

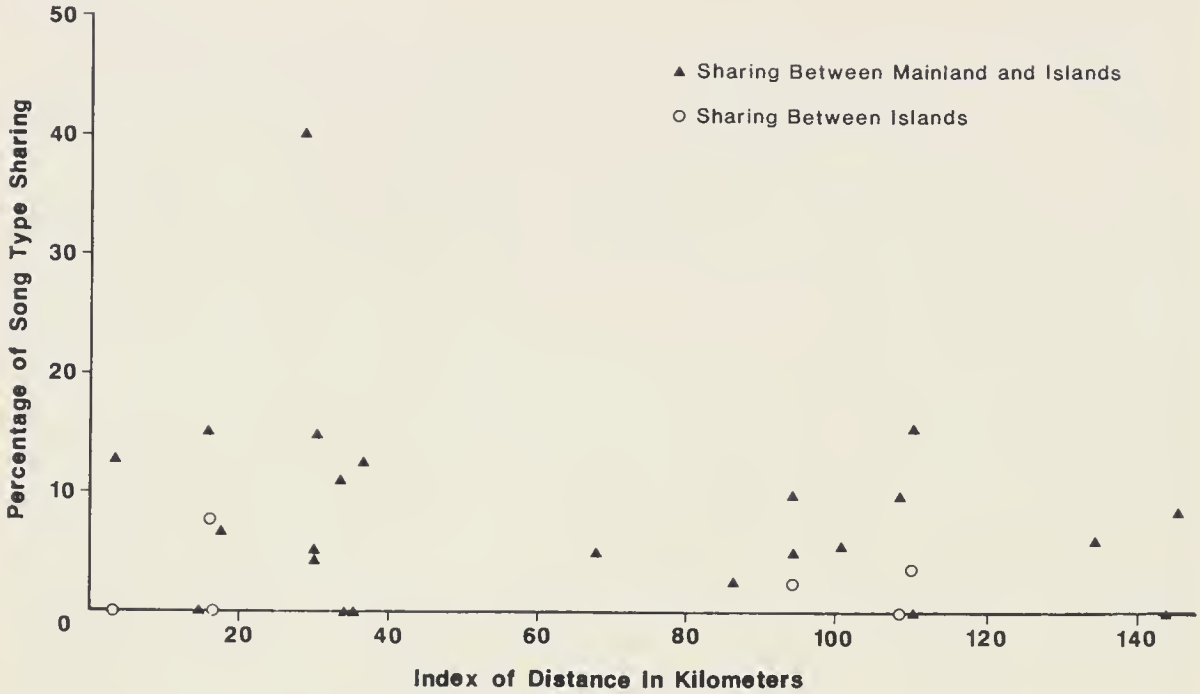

FIG. 3. Percentage song sharing between sites separated by water barriers as a function of distance separating them.

DISCUSSION

Song-type distribution.—The distribution of song types we observed for the Carolina Wren is similar to that reported for other species of oscines with repertoires. For example, Bitterbaum and Baptista (1979) examined syllable repertoires of male House Finches (*Carpodacus mexicanus*) up to 5-km apart and found a significant negative correlation (−0.95) between the extent of syllable sharing and distance. Kroodsma (1974) suggested a similar relationship for Bewick's Wrens (*Thryomanes bewickii*) up to about 6-km apart. In sedentary species, especially those occupying permanent territories such as the Carolina Wren, geographic isolation appears to be equivalent to acoustic isolation. That is, in our study, a water barrier sufficient to keep birds at two sites from hearing one another resulted in a divergence of song types similar to that noted in males a much greater distance apart on mainland sites with continuous populations.

The extent of song sharing between wrens on islands and mainland sites indicates that a water barrier reduces, but does not completely prevent dispersal (Table 2). The percentage of sharing between wrens on Poplar Island and the adjacent mainland, 3-km distant, was 12.4%; equivalent to wrens separated by 145 km on continuous mainland sites. One mainland individual (Table 1, No. 4), however, had 8 song types not found in the repertoires of any of the other mainland males. Of these, 3 were found only in Poplar Island males, indicating probable emigration from the island to the adjacent mainland.

TABLE 2
SONG-TYPE SHARING BETWEEN SITES FOR 309 TOTAL SONG TYPES AT FOUR ISLAND AND SEVEN MAINLAND SITES

Song type found at:	Number types	%
One site	242	78
Mainland	116	38
Island	126	41
Two sites	39	13
Mainland	11	4
Island	8	3
Both	20	7
Three sites	16	5
Mainland	3	1
One mainland and two island	3	1
Two mainland and one island	10	3
Four sites	6	2
Three mainland and one island	5	2
Two mainland and two island	1	<1
Five sites	2	1
Three mainland and two island	1	<1
Four mainland and one island	1	<1
Six sites	3	1
Four mainland and two island	3	1
Seven sites	1	<1
Five mainland and two island	1	<1

The sharing of song types is an indicator of continuity or connectivity between individuals in a population. Individuals in disjunct or separated populations are expected to share song types only if an exchange of individuals has occurred at some time in the past. As adult Carolina Wrens are sedentary, this exchange likely is due to natal dispersal. Song learning takes place during the first 3 months of life (Helgeson 1980, Morton et al. 1986). Adults do not add new song types even if they are artificially moved to sites where they interact with live songsters using different songs (Morton et al. 1986). Thus dispersing juveniles can carry song types learned before dispersal to new areas. Still, most song types (242 or 78% of the total sample of 309) were restricted to single sites. In contrast, four types (1%) were found nearly everywhere (Table 2); this cannot be accounted for by the natal dispersal argument.

There is no obvious morphological similarity in the widespread song types that might correlate with their broad distribution (Chu 1979, Table

TABLE 3

MEASUREMENTS (MEAN ± SD) OF THE FOUR WIDESPREAD SONG TYPES COMPARED TO THE SAME MEASURES ON THE REMAINING SAMPLE (305 SONG TYPES)

Song type[a]	Elements per syllable	Highest frequency (kHz)	Lowest frequency (kHz)	Syllable duration (msec)	Intersyllable duration (msec)	Freq. range (kHz)	N
18	5.2 ± 0.7	6.0 ± 0.4	1.6 ± 0.2	334 ± 18	53 ± 7	4.3 ± 0.5	12
35	4.2 ± 0.5	5.4 ± 0.7	1.9 ± 0.1	222 ± 25	43 ± 11	3.5 ± 0.6	12
50	4.8 ± 0.8	5.0 ± 0.5	1.3 ± 0.1	320 ± 39	46 ± 13	3.7 ± 0.5	15
67	3.9 ± 0.6	5.3 ± 0.5	1.5 ± 0.2	207 ± 23	46 ± 10	3.8 ± 0.5	15
$\bar{x}$[b]	4.6 ± 0.8	5.4 ± 0.6	1.6 ± 0.3	276 ± 70[d]	48 ± 11[d]	3.9 ± 0.6	54
$\bar{y}$[c]	4.8 ± 0.2	5.5 ± 0.2	1.6 ± 0.1	333 ± 74	59 ± 23	3.9 ± 0.2	679

[a] Refers to the number assigned to song types in Chu (1979).

[b] Means for the four widespread song types, calculated from the entire sample of 54 song examples rather than as the mean of the four means.

[c] Refers to the means for the 679 song examples of the remaining 305 song types.

[d] Significantly different from the grand mean ($\bar{y}$) using a one-tailed t-test, $P < 0.0005$. The remaining values do not differ.

3). Syllable duration and intersyllable intervals in our four most widespread songs, however, are significantly shorter than the rest of the sample (Table 3). Perhaps these songs are widespread because they suffer little degradation in many habitats (Gish and Morton 1981). If Northern Mockingbirds (*Mimus polyglottus*) mimic these preferentially, Carolina Wrens might learn them. This might explain how these songs reach the islands so readily since mockingbirds regularly leave the islands in the winter and return to them in the spring (pers. obs.).

The distribution of song types in Carolina Wrens indicates a tendency for songs to be restricted to a single site, akin to dialects, but some (22%) songs are widespread to varying degrees. A small percentage of the song types (1% in this study) were found at all sites. Songs shared between individuals at different sites likely result from natal dispersal. Still, the restricted geographic range of most song types indicates a strong tendency for males to copy songs from others, with whom, after natal dispersal, they will compete territorially.

Song sharing among neighbors.—The advantage of sharing songs with neighbors has been discussed elsewhere (Shy and Morton 1986, Morton 1982, 1986). Morton et al. (1986) showed that 4 naive young wrens preferentially learn undegraded songs, acquiring repertoires largely consisting of such songs (71–89%). Undegraded song is equivalent to neighbor song, as mentioned above (see also McGregor and Krebs 1984, Shy and Morton 1986). If 71–89% of a wren's song repertoire results from an innate predisposition to learn undegraded songs, then a bird with an

average repertoire size of 32 song types is predicted to learn from 23 to 28 songs from neighbors and from 4 to 9 song types from nonneighbors. These latter song types would either be unique to the individual (i.e., learned at its natal site and not found in its breeding site or through mimicry of other species) or not shared with immediate neighbors.

If the average preference for undegraded songs of 80% found by Morton et al. (1986) is multiplied by the total number of song types noted in the present study, 309, we obtain a value of 247. This is the number of song types that should be limited to immediate neighbors and, therefore, to one site. As we reported above, 242 of the 309 song types were restricted to one site, only 2% different from the predicted value. In other words, our site ("population") data may be explained at the level of individual birds exposed only to song types heard from different distances (i.e., more or less degraded). Thus, data showing that 78% of the song types are restricted to a single site may be the result of individual interactions among birds within hearing distance of one another. An alternate idea, that site-restricted songs serve to restrict gene flow (e.g., Baker 1975), has not been tested.

The ranging hypothesis (Morton 1986) predicts that the extent to which song types are shared will increase with increased neighborhood stability. With such stability there will be less selective pressure favoring the acquisition of unshared song types. This prediction is testable because the Carolina Wren ranges into warmer climates where the large, unpredictable, winter die offs found in our Maryland study site do not occur (Morton and Shalter 1977).

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TERRITORIAL RESPONSES TO SONG PLAYBACK IN ALLOPATRIC AND SYMPATRIC POPULATIONS OF ALDER (*EMPIDONAX ALNORUM*) AND WILLOW (*E. TRAILLII*) FLYCATCHERS

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ABSTRACT.—Previous studies have shown little response of territorial Alder (*Empidonax alnorum*) and Willow (*E. traillii*) flycatchers to heterospecific song playback within their range of breeding overlap, suggesting the absence of interspecific territoriality. However, the same species clearly exhibit interspecific breeding territories in shared habitats in southern Ontario. Such conflicting observations may have resulted from previous studies being conducted in habitats where only one of the species was present. In an attempt to reconcile these different observations, the responses of both species to heterospecific song playback in sympatric and allopatric populations were compared near Guelph, Ontario. I hypothesized that aggressive responses to heterospecific song should occur only in shared habitats. Both species took significantly less time to approach, moved closer, and spent more time near the sound source, and more frequently elicited aggressive vocalizations in response to heterospecific song in shared habitats. The virtual absence of response by either flycatcher in allopatric populations suggests that both species learn, through coexistence, to recognize the heterospecific song as that of a potential competitor. In addition, the responses of Willow Flycatchers to both con- and heterospecific song were more aggressive than that of the Alder. Recent range expansions of the Willow Flycatcher into areas historically occupied by the Alder Flycatcher may in part be due to interspecific dominance. *Received 9 Sept. 1986, accepted 18 Mar. 1987.*

Numerous studies have shown that bird species with similar feeding ecology defend interspecific territories (Orians and Willson 1964, Cody 1969, Gorton 1977, Reed 1982), and respond aggressively to tape playbacks of heterospecific song types (Emlen et al. 1975, Gorton 1977, Reed 1982). A few investigators have observed that the aggressive response towards interspecific song types is more intense in areas where ecologically similar species occur together, but may be absent in allopatric ranges (Emlen et al. 1975, Falls 1978, Catchpole and Leisler 1986). Such observations suggest that the recognition of close competitors is dependent on prior competitive experience with heterospecific individuals (Falls and Szijj 1959, Catchpole 1978, Richards 1979, Catchpole and Leisler 1986).

The Alder (*Empidonax alnorum*) and Willow (*E. traillii*) flycatchers are morphologically almost identical sibling species of different song types (Willow: *fitz-bew*; Alder: *fee-bee-o*) that frequently coexist in habitats within their range of breeding overlap (Zink and Fall 1981, Barlow and

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McGillivray 1983). Both species feed primarily on invertebrates, and, where they coexist, use similar foraging strategies (Barlow and McGillivray 1983). Hence, competition for food between these species, if it occurs, should be maximal in shared habitats, and selection should favor the development of interspecific territories (Orians and Willson 1964). This prediction is supported by observations made during a two-year study of the territorial behavior of the Willow Flycatcher in southern Ontario (Prescott 1986): both species vigorously excluded the other from their breeding territories. In contrast, both Stein (1958, 1963) and Barlow and McGillivray (1983) have reported that during playback experiments within the range of sympatry, both species tended not to respond agonistically to the heterospecific song. It is not clear from these studies, however, whether or not both species coexisted in all habitats where experiments were conducted, although in a few instances, Stein (1958:22, 1963:34) reported that certain males of both species responded to playback of both song types, implying occupation of shared habitat.

If prior experience with the heterospecific song is necessary for the development of interspecific territoriality, it is possible that earlier studies were completed, for the most part, in habitats containing only a single *Empidonax* species. In this study, I report the responses of Alder and Willow Flycatchers to tape playback of conspecific and heterospecific songs in both exclusive (allopatric) and shared (sympatric) habitats. I hypothesized that if the recognition of a close competitor is a learned response, then agonistic behavior directed towards the heterospecific song type, and therefore interspecific territoriality, should occur only in sympatric populations.

METHODS

Playback experiments were conducted at 8 sites within 35 km of Guelph, Ontario (43°32′N, 80°13′W), during the breeding season of 1985. Willow and Alder flycatchers occurred allopatrically in three and two habitats, respectively, and sympatrically in three habitats. Other sites in the region supported flycatcher populations, but because interspecific recognition might result from cohabitation with a heterospecific during previous breeding seasons (Emlen et al. 1975), only those habitats where the composition of flycatchers was known to be similar over two breeding seasons were chosen for investigation. Allopatric and sympatric flycatcher populations were separated by at least 3 km to minimize the possibility of contact between populations.

Because territorial defense in Alder and Willow flycatchers is achieved primarily through song (Stein 1958), and because these species are virtually identical in appearance, I consider here only the responses to auditory stimuli. A 150-sec tape of each song type (approx. 10 songs/min) was assembled from commercially available bird song records (Peterson 1975, National Geographic Society 1983), and played to territorial flycatchers in the field on a Sanyo model M2566 portable cassette recorder. Because territorial response to song in flycatchers varies with the time of the breeding season (Barlow and McGillivray 1983), trials

were conducted only during the month of June, corresponding to the nest building and incubation periods of these species (Bent 1942, pers. obs.). A 3-in (7.6-mm) speaker was projected vertically from the approximate center of the territory under investigation (see Prescott 1986 for details on territory mapping), at a 10–12 m distance from the observer. Both song types were played to the same territory holder approximately 30 min apart, the order of presentation being determined by a coin toss. Playback began when the male was seen advertising from a prominent perch >30 m from the speaker. The tape was played to completion, during which time the following responses of the territory holder were recorded: (1) time taken by the bird to approach to within 8 m of the speaker (only if accompanied by aggressive vocalizations or displays, see below), (2) closest distance approached, (3) time spent within <3 m of the speaker, (4) number of *whit* calls, (5) number of *wee-oo* calls, (6) number of *churr* calls, and (7) presence of attacks (threat displays <0.25 m from speaker). The above vocalizations are common to both species, and represent increasing levels of agitation (Stein 1958, pers. obs.).

Individual birds were tested from 2 to 5 times during the study period. In order to prevent habituation to songs (Weeden and Falls 1959, Emlen 1972), a period of at least 5 days was allowed between playback sessions. Responses of each species to conspecific and heterospecific songs were pooled for sympatric and allopatric populations, and compared using Mann-Whitney *U*-tests (Sokal and Rohlf 1969). In addition, I compared the relative responses of Willow and Alder flycatchers to their own song with responses to the opposite pattern of song. This was done in order to test whether the response of the Willow is, in general, more intense than that of the Alder (Stein 1963).

RESULTS

Of 98 playback experiments conducted during the study period, 53 were conducted on 15 individual Willow Flycatchers (8 sympatric, 7 allopatric) and 45 on 13 Alder Flycatchers (6 sympatric, 7 allopatric). Responses to tape playback were essentially "all or nothing." Birds that did not respond either remained on their perch without vocalizing, or engaged in other activities without approaching the speaker. Birds that responded to either song type typically did so immediately. The first response of a perched bird was usually to orient towards the speaker, with an accompanying increase in the frequency of *whit* or *wee-oo* calls. Flights towards the sound source usually occurred within 10 sec of the initiation of the playback, and were followed by frequent perch changes and short flights over and around the speaker. *Churr* calls were usually only given within 4 to 5 m of the speaker, and were accompanied by agonistic body postures including crest-raising, feather-spreading, tail-pumping, and wing vibrations (see Stein 1958). Agitated birds usually moved away (>10 m) from the speaker after 60 to 90 sec, but continued to vocalize for the duration of the test.

Responses to heterospecific song type.—There were clear differences between sympatric and allopatric populations of both species in the responses to heterospecific song playback (Table 1). Both Alder and Willow

TABLE 1

RESPONSES OF ALDER AND WILLOW FLYCATCHERS (MEAN ± SE) TO HETEROSPECIFIC SONG PLAYBACK IN SYMPATRIC AND ALLOPATRIC POPULATIONS NEAR GUELPH, ONTARIO

Response	Alder response to Willow song			Willow response to Alder song			Species comparison[b]
	Sympatry (N = 24)	Allopatry (N = 21)	P[a]	Sympatry (N = 29)	Allopatry (N = 24)	P[a]	
Time to approach <8 m (sec)	19.8 ± 1.7	133.2 ± 9.2	<0.0001	19.7 ± 1.8	122.9 ± 11.1	<0.0001	>0.05
Closest distance (m)	3.3 ± 0.3	15.3 ± 1.5	<0.0001	3.7 ± 0.4	13.2 ± 1.5	<0.0001	>0.05
Number of *whits*	12.5 ± 0.8	4.1 ± 0.8	<0.0001	14.2 ± 1.0	5.2 ± 0.9	<0.0001	>0.05
Number of *wee-oos*	5.3 ± 0.6	1.5 ± 0.4	<0.0001	8.1 ± 0.7	2.2 ± 0.7	<0.0001	<0.005
Number of *churrs*	3.6 ± 0.4	0.7 ± 0.2	<0.0001	5.7 ± 0.6	1.8 ± 0.7	<0.0001	<0.05
Time spent <3 m (sec)	8.5 ± 1.6	0.0 ± 0.0	<0.0001	7.4 ± 1.6	2.6 ± 1.5	<0.05	>0.05
Number of tests with attacks	1	0	—	2	1	—	—

[a] Probability of species difference in response between sympatric and allopatric populations.
[b] Probability of species difference in sympatric populations.

TABLE 2
COMPARATIVE RESPONSES (MEAN ± SE) OF TERRITORIAL ALDER AND WILLOW FLYCATCHERS TO CONSPECIFIC SONG PLAYBACK

Response	Alder Flycatcher (N = 45)	Willow Flycatcher (N = 53)	P[a]
Time to approach <8 m (sec)	18.8 ± 1.0	13.0 ± 0.9	<0.0001
Closest distance (m)	3.4 ± 0.2	3.4 ± 0.3	>0.05
Number of *whits*	14.4 ± 0.8	18.7 ± 0.9	<0.01
Number of *wee-oos*	4.5 ± 0.4	10.1 ± 1.7	<0.0001
Number of *churrs*	3.4 ± 0.4	7.0 ± 0.5	<0.0001
Time spent <3 m (sec)	8.1 ± 1.6	10.9 ± 1.7	>0.05
Number of tests with attacks	1	4	—

[a] Probability of a species difference using Mann-Whitney *U*-tests.

flycatchers responded much more aggressively ($P < 0.05$) in all behavioral categories to the heterospecific song in habitats where both species were present than where only one species occurred. In general, responses by birds to the opposite song were absent in allopatric populations, although a single Alder Flycatcher did respond to the Willow song in each of the 3 trials it was involved in. Two Willow Flycatchers in allopatric areas also responded aggressively to heterospecific playback during all of the trials (N = 2 and 3) in which they were included, and one of the birds attacked the speaker. Such levels of aggressive behavior were rare, however, being observed only once in sympatric populations by Alder, and twice by Willow flycatchers in response to the opposite song form. Because of the nonindependence of the data resulting from pooling data for individual birds tested repeatedly during playback experiments, and because the responses of individuals of both species were consistent throughout the study (with respect to the presence or absence of aggressive responses), the responses to heterospecific song playback for both species were reanalyzed using a Fisher's exact test (Seigel 1956). For both species, responses were significantly more frequent in sympatric populations (Alder Flycatcher, $P < 0.005$; Willow Flycatcher, $P < 0.01$), confirming the results of the previous analysis.

A comparison of responses to heterospecific song between species (sympatric populations only) showed that Willow Flycatchers more frequently produced *wee-oo* ($P < 0.005$) and *churr* calls ($P < 0.05$) than did Alder Flycatchers. There were no significant differences with respect to the other measured behaviors ($P > 0.05$).

Responses to conspecific song type.—A comparison of responses obtained from all populations for both species (Table 2) shows that Willow Flycatchers took less time to approach within 8 m of the speaker ($P <$

0.0001), and made more frequent use of aggressive vocalizations (*whit* calls, $P < 0.01$; *wee-oo* and *churr* calls, $P < 0.0001$) than did the Alder Flycatcher. In addition, Willow Flycatchers attacked the speaker in 4 of 53 playback trials (7.5%), compared to 1 attack in 45 trials (2.2%) for Alder Flycatchers.

DISCUSSION

Aggressive responses to heterospecific song playback in these closely related flycatchers occurred more frequently in habitats where both species bred. Because the choice of habitats was designed to reflect previous experience (or inexperience) with the sibling species, it appears that the development of response to heterospecific song in Alder and Willow flycatchers represents a learned behavior (see also Emlen et al. 1975; Catchpole 1978; Falls 1978, 1982; Catchpole and Leisler 1986). The differences in response of individuals in sympatric and allopatric populations also suggest that although the songs of the two species are phonetically similar, both species are able to discriminate between their song types. Hence, interspecific aggression apparently did not occur as a result of "mistaken identity" as has been proposed for other species pairs demonstrating interspecific territoriality during the breeding season (Murray 1971, 1976, 1981). The two Willow and the single Alder flycatchers that responded to playback of heterospecific song in allopatric populations represent notable exceptions. It is unknown whether these individuals responded to the opposite song form because of an inability to distinguish it from their own song (i.e., mistaken identity), or because they recognized the "intruder" as an ecologically similar, potentially competing species. The latter could occur if these individuals had learned the other species' song by sharing habitats during previous breeding seasons (Emlen et al. 1975).

The occurrence of interspecific song recognition and aggression are contrary to the observations of both Stein (1958, 1963) and Barlow and McGillivray (1983), who found little or no response of either species to heterospecific song playback. My results suggest that previous experience with the related species through coexistence might be one explanation for the discrepancy; however, because at least some of the previous playback studies were conducted in sympatric flycatcher populations, the lack of any interspecific aggression is unexpected, and interspecific territoriality may have been absent in previously considered habitats. If competition for food has been important in the evolution of territoriality between ecologically similar species (Orians and Willson 1964, Cody 1969), long-term differences in the abundance of insect food available to different flycatcher populations may reflect the presence or absence of aggressive responses. Barlow and McGillivray (1983) suggested that the foraging behavior of Willow and Alder flycatchers was not limited by food avail-

ability in the habitats where they conducted playback experiments (also in southern Ontario). At least for Willow Flycatchers, however, food was apparently not limiting in habitats considered in the present study (Prescott 1986). Hence, differences in food abundance on a short-term basis cannot account for differences in the observed aggression between Alder and Willow flycatchers in studies conducted to date.

Methodological differences are known to affect the outcome and comparability of song-playback studies (Falls 1978, Kroodsma 1986). During the course of studies on *Empidonax* flycatchers near Guelph, it was apparent that song tapes (other than those assembled for the present study) that were recorded at too high a volume, or played back at too low or high a volume frequently failed to elicit aggressive responses, even to conspecific song. Similarly, songs from speakers placed only a short distance outside the territory under observation were often ignored by the occupant. Because of the only brief accounts of playback methodology provided in earlier studies, the extent to which such factors influenced the difference in responses observed between our studies is unclear. Nevertheless, the presence or absence of previous experience with heterospecific flycatchers remains the most plausible explanation for the results generated here, and are consistent with observations on other interspecifically territorial species pairs (Emlen et al. 1975, Catchpole 1978, Falls 1978, Catchpole and Leisler 1986).

My analyses also show that Willow Flycatchers tended to react more aggressively to both conspecific and heterospecific song playback than did Alder Flycatchers. This supports Stein's (1963) contention that the former species is behaviorally dominant to the latter. This is also supported by anecdotal field observations of aggressive encounters between these species made during 1984 and 1985. Seven aerial conflicts were recorded, all of which resulted in the Willow Flycatcher successfully expelling the Alder from the disputed area. Four of 7 such encounters were known to be the result of intrusions by Willow Flycatchers onto Alder territories, and 4 of 5 were known to have been initiated by Willow Flycatchers. In addition, three Alder Flycatcher territories were known to have been usurped by adjacent Willow Flycatchers early in the breeding season (2 in 1984, 1 in 1985). Alder Flycatchers that lost their territories in this manner apparently did not remain in the vicinity to breed. Therefore, the Willow Flycatcher may be sufficiently dominant to expel the Alder from shared habitats. Thus, the defense of interspecific territories is clearly of benefit to the Willow Flycatcher, but apparently is not to the Alder. This is in contrast to the assumptions of the mistaken identity theory of interspecific territoriality, where such interactions are considered to be nonadaptive to both participants (Murray 1971, 1976, 1981). These behavioral observations therefore reinforce the conclusion that interspecific territori-

ality between these flycatchers cannot be the result of misdirected intraspecific aggression.

The observed interspecific dominance of the Willow Flycatcher might have demographic implications. Stein (1963) has suggested that the Alder Flycatcher presently is contracting northward, being replaced by the northwardly expanding Willow. Recent habitat alteration associated with agricultural practices has been attributed to bringing these species into secondary contact, and may be partly responsible for the suspected range changes (Stein 1963). However, Gauthreaux (1978, 1982) has argued for the importance of intraspecific behavioral dominance in determining age and sex class distributions of certain temperate-zone birds during the nonbreeding season. The results presented here suggest that interspecific dominance might also be an important factor in the recent expansion of Willow Flycatchers into areas historically occupied by the Alder Flycatcher.

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VARIATION IN THE BOUNCE AND WHINNY SONGS OF THE EASTERN SCREECH-OWL

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ABSTRACT.—Intra- and interindividual variation in the "bounce" and "whinny" songs of Eastern Screech-Owls (*Otus asio*) in central Kentucky were examined. Significant interindividual variation was noted in each character examined. Temporal characters generally were more variable than frequency characters in "whinny" songs, but the reverse was found to be true for "bounce" songs. Interindividual variation was also noted in the structure of notes used in "bounce" songs. The "bounce" songs of females were significantly longer in duration and higher in frequency than those of males. Our results suggest that there is sufficient variation in these songs to permit sexual and individual recognition. *Received 20 Jan. 1987, accepted 6 May 1987.*

The song repertoire of Eastern Screech-Owls (*Otus asio*) includes the "whinny" (primary song) and the "bounce" (secondary song). Previous investigators have reported both individual and geographic variation in these songs. Lynch and Smith (1984) noted that differences in the frequency of songs could be used to determine if owls being surveyed were new or had been counted previously. Andrews et al. (1982), using playback to count Eastern Screech-Owls in Massachusetts, reported that responding owls exhibited considerable variation in the frequency of the tremolo ("bounce" song). Marshall (1967) reported regional variation in the "whinny" song. Here we examine intra- and interindividual variation in the "bounce" and "whinny" songs of Eastern Screech-Owls in central Kentucky.

METHODS

Recordings of 24 Eastern Screech-Owls were made from 21 May to 3 July 1984 and from 16 June to 20 August 1985 in Madison County, Kentucky. Most recordings were made at the Central Kentucky Wildlife Management Area, 17 km SSE of Richmond, Kentucky. Additional recordings were made in an area 3.7 km SSW of Richmond. All recordings were of songs uttered in response to the playback of "bounce" and "whinny" songs. Playback tapes were made using (1) recordings of screech-owls obtained in the study area and (2) owl songs in "A field guide to bird songs of eastern and central North America" (Anonymous 1975). Recordings were sometimes obtained during and after playback experiments performed in conjunction with another study (Cavanagh 1986). During these experiments the "bounce" songs of neighboring and nonneighboring owls were played for 5 min. On other occasions songs were broadcast for as long as 15 min.

Eight owls were captured and fitted with radiotransmitters to aid in individual identification. Transmitters were attached backpack style (Smith and Gilbert 1981) using nylon

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TABLE 1
VARIATION IN NINE VARIABLES OF "BOUNCE" SONGS

Variable	N[a]	Minimum	Maximum	Mean	SD	CV
Notes/song	22	25.10	39.74	32.30	3.42	10.59
Duration (sec)	22	1.70	2.66	2.30	0.24	10.30
Notes/sec	22	12.71	15.00	14.05	0.68	4.87
Initial frequency[b]	20	364	949	723	124	17.10
End frequency	20	398	944	721	115	15.99
Maximum frequency	20	441	999	754	120	15.89
Minimum frequency	20	364	929	708	117	16.53
Frequency range	20	19	76	48	15	31.68
Mean frequency	20	414	983	735	120	16.27

[a] N = number of individuals. For the first 3 variables, 411 songs were analyzed (range = 7–30 songs/individual). For all frequency variables, 200 songs were analyzed (10 songs/individual).
[b] All frequency measurements in Hertz.

cord. Owls were captured by (1) taking them from nest boxes or natural cavities or (2) luring them into a mist net using playback of "bounce" songs. The sex of several captured owls was determined by (1) the presence or absence of an incubation patch and (2) behavior during the nesting season. During this time, females generally roost in nest cavities (either incubating eggs or brooding nestlings) while males often roost in nearby trees (pers. obs.).

Owls with transmitters were often recorded on several different occasions, sometimes over a period of more than a year. Recordings of owls without transmitters were obtained once at one location.

All recordings were made using a Uher 4000 Report Monitor tape recorder at a tape speed of 4.7 or 9.5 cm/sec with a Dan Gibson parabolic microphone. Songs were analyzed using a Kay Elemetrics Co. Sona-Graph (Model 6061A) at the wide band-pass setting. Measurements of the duration of entire songs, individual notes, and internote intervals were made using a ruler. A note was defined as a continuous trace on a sonagram. Frequency measurements were made to the nearest 25 Hz using a transparent overlay. All analyses were performed using the Statistical Analysis System (SAS Institute 1985) General Linear Model for unbalanced data.

RESULTS

"Bounce" songs are composed of a series of notes repeated at a constant or nearly constant frequency (Fig. 1A, B) (Table 1). The mean duration [±SD] of individual notes was 30.32 ± 6.06 msec (N = 5982) while the mean internote interval was 25.01 ± 3.79 msec (N = 5796) in duration. The duration of successive notes within bounce songs differed significantly ($F = 93.34$, $P < 0.001$). Typically, the duration of successive notes increased in the first part of a song, peaked, then decreased (Figs. 1, 2). The longest note in a typical bounce song was 1.86 times as long (N = 20 owls, Range = 1.55–2.50) as the shortest note. The duration of successive internote intervals also varied within songs ($F = 52.39$, $P < 0.001$).

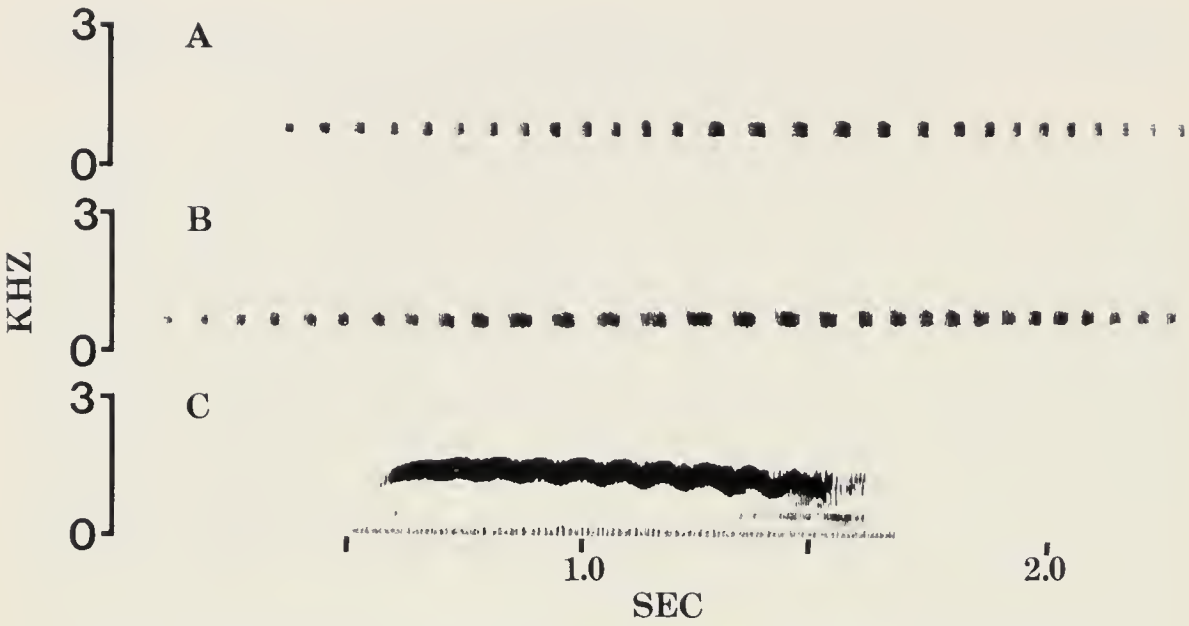

FIG. 1. The "bounce" (A, B) and "whinny" songs (C) of Eastern Screech-Owls.

Internote duration typically was longer at the beginning and again at the end of a "bounce" song (Figs. 1A, B; 2). Individual differences were observed in the pattern of variation for both note and internote duration (Fig. 3). For all owls combined (N = 20) the note with the longest duration was note 15 (Fig. 2); however, among individuals the note with the longest duration ranged from note 5 to note 25 (Fig. 3). Although the internote duration was generally longest at the very beginning of a "bounce" song, a second peak in internote duration was always observed. This second peak corresponded to the peak in note duration (Fig. 2).

Much interindividual variation in "bounce" songs was apparent. One-way analysis of variance revealed significant individual differences ($P < 0.001$) for every parameter examined, with frequency variables exhibiting more interindividual variation than temporal variables (Table 1). Within individuals, frequency was relatively constant while temporal variables (duration and number of notes per song) exhibited more variation. A comparison of coefficients of variation indicated that intraindividual variation was consistently less pronounced than interindividual variation.

Interindividual variation in note structure was also observed (Fig. 1A, B). Individual owls consistently uttered notes with the same structure. Two individuals that we recorded over a period of more than one year showed no change in the structure of "bounce" song notes.

Significant differences were observed in the "bounce" songs of male (N = 5) and female (N = 3) screech-owls (Table 2). The "bounce" songs of females were significantly longer in duration and higher in frequency

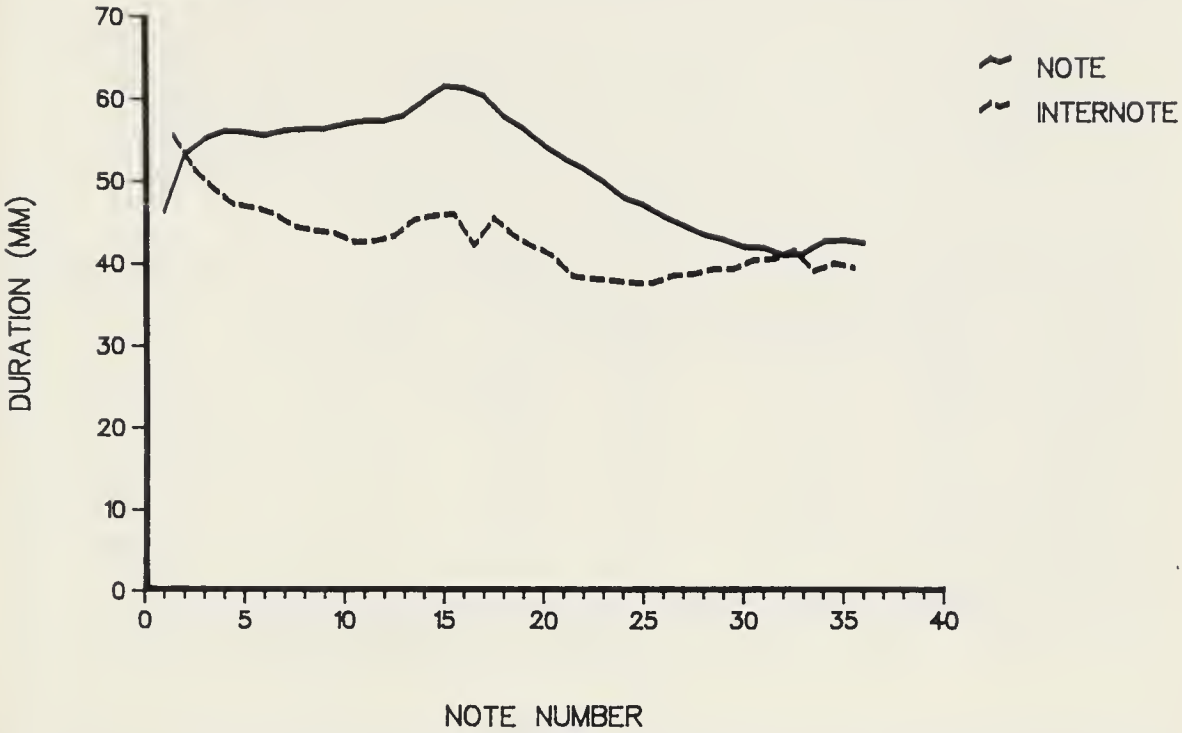

FIG. 2. Mean note and internote durations in the "bounce" songs of 20 Eastern Screech-Owls combined (N = 10 per owl).

than those of males. Females also uttered notes at a significantly slower rate than did males (Table 2).

The "whinny" song has been described as a "quavering whistle (monotone or descending)" (Robbins et al. 1983:174). Typically, the initial part of the song exhibited a slight increase in frequency, while the latter part of the song was characterized by a gradual decrease in frequency (Fig. 1C). The last part of "whinny" songs often exhibited a series of rapid frequency modulations (Fig. 1C). One-way analysis of variance revealed significant individual differences ($P < 0.001$) for every parameter examined (Table 3).

In contrast to "bounce" songs, temporal characters generally were more variable than frequency characters in "whinny" songs (Table 3). As with "bounce" songs, coefficients of variation consistently revealed less intra- than interindividual variation in "whinny" songs.

DISCUSSION

Previous authors have suggested that the songs or calls of Eastern Screech-Owls may exhibit individual variation (Andrews et al. 1982, Lynch and Smith 1984). Weyden (1975) examined the "bounce" songs of several individuals and reported variation in the highest (maximum) frequency,

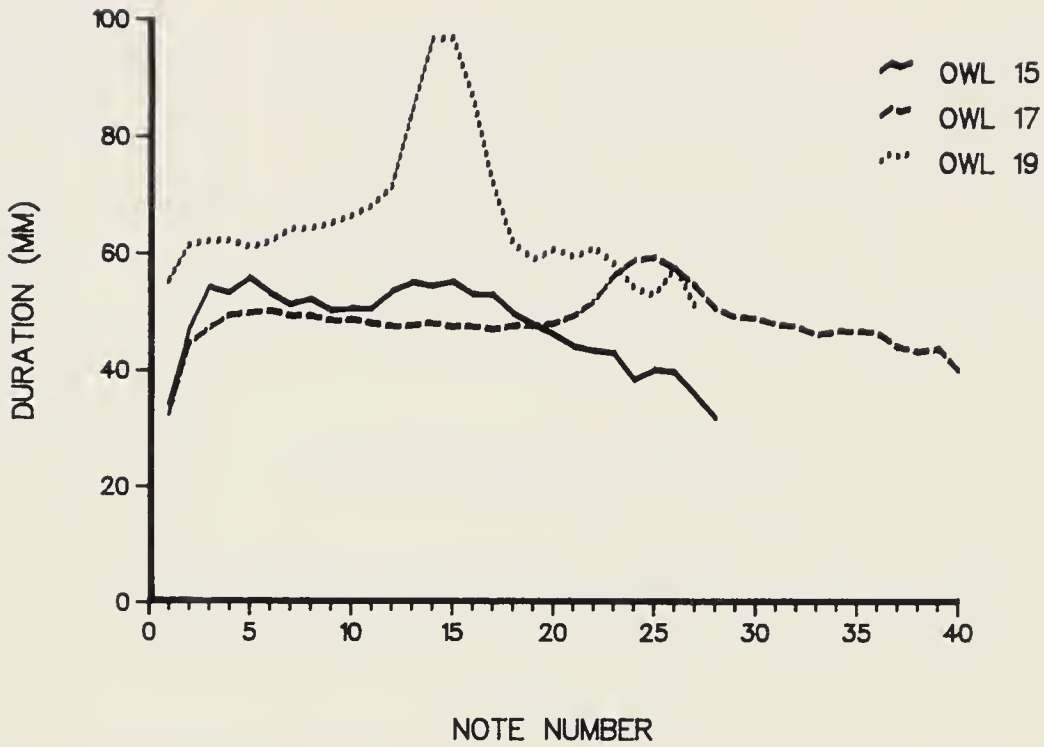

FIG. 3. Mean note durations in the "bounce" songs of three Eastern Screech-Owls (N = 10 per owl).

number of notes per second, and number of notes per motif (song). Our results are consistent with those of previous studies. Significant interindividual differences were noted in every parameter of "bounce" and "whinny" songs examined, and significant differences were also noted between the "bounce" songs of males and females. Temporal variables appeared to be more variable among individuals than the frequency variables. Variation in the duration of "bounce" songs (and, therefore, in the number of notes per song) may in part be correlated with level of "excitement." Owls generally uttered more notes per song after "bounce" songs were played back for at least five min than they did in response to playbacks of shorter duration (Cavanagh 1986).

The "bounce" songs of male and female Eastern Screech-Owls differ in frequency, with the songs of females being higher in pitch. Such differences have been noted by previous investigators (Miller 1934, Weyden 1975). This difference may allow owls to determine quickly the sex of singing conspecifics. "Bounce" and "whinny" songs also exhibited much interindividual variation, with certain features being more variable than others. Relatively stereotyped features may be useful for species recognition, while more variable features may be important for individual recognition (Falls 1982). Our analysis revealed several features of "bounce" and "whinny" songs that would appear to exhibit sufficient variation to

TABLE 2

VARIATION IN "BOUNCE" SONGS OF MALE AND FEMALE EASTERN SCREECH-OWLS

Variable	Males[a]		Females[b]			
	Mean	CV	Mean	CV	*F* ratio	*P*
Song duration (sec)	2.14	12.22	2.72	16.16	39.66	<0.001
Notes/song	30.79	11.36	33.89	8.53	7.58	<0.05
Notes/sec	14.42	3.62	12.54	7.99	202.75	<0.001
Initial frequency[c]	717	5.33	825	8.03	100.36	<0.001
End frequency	720	5.56	800	5.16	77.21	<0.001
Minimum frequency	709	5.60	795	5.64	78.98	<0.001
Maximum frequency	739	4.19	839	7.16	121.65	<0.001
Frequency range	33	39.93	46	31.09	8.81	<0.05
Mean frequency	721	4.21	823	6.80	146.02	<0.001

[a] N = 5. A total of 110 songs was analyzed (range = 10–30 songs/individual for duration, notes/song, and notes/sec; 10 songs/individual for all frequency variables).
[b] N = 3. A total of 22 songs was analyzed (10, 8, and 4 songs, respectively).
[c] All frequency measurements in hertz.

allow screech-owls to determine the individual identity of singing conspecifics. Further study is needed, however, to determine if such recognition occurs and, if so, which features of these songs are involved.

The vocalizations of non-oscines have sometimes been described as variable and highly graded (e.g., Huxley and Wilkinson 1977, Mace 1981). Several investigators, however, have reported on non-oscines in which calls or songs are relatively discrete (Beightol and Samuel 1973, Miller 1978, Wooller 1978, Hand 1981, Saunders 1983, Pietz 1985, and others).

TABLE 3

VARIATION IN NINE VARIABLES OF "WHINNY" SONGS

Variable	N[a]	Minimum	Maximum	Mean	SD	CV
Song duration[b]	11	0.94	1.50	1.15	0.16	14.16
Duration (nonmodulating)	11	0	0.48	0.19	0.15	78.30
Duration (modulating)	11	0.60	1.35	0.96	0.22	22.98
Number of modulations	11	6.59	18.29	12.78	3.75	29.31
Initial frequency[c]	11	1.015	1.411	1.213	0.111	9.15
End frequency	11	0.827	1.118	0.946	0.102	10.76
Maximum frequency	11	1.199	1.680	1.420	0.135	9.44
Minimum frequency	11	0.820	1.062	0.932	0.093	9.99
Frequency range	11	0.230	0.725	0.488	0.158	32.29

[a] N = number of individuals. A total of 152 songs was analyzed (range = 4–32 songs/individual).
[b] All duration measurements in seconds.
[c] All frequency measurements in kilohertz.

Our results indicate that the songs of Eastern Screech-Owls are also discrete, exhibiting less intra- than interindividual variation. Previous authors have noted that sounds used over long distances tend to be more discrete than sounds used at short distances (Marler 1967, Morton 1982). The songs of Eastern Screech-Owls are used in long-distance communication, as are the relatively discrete vocalizations of many other non-oscines. The variable, highly graded vocalizations of non-oscines appear to be those used at short distances.

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COMPARISONS BETWEEN MORPHOMETRIC AND GENETIC DIFFERENTIATION AMONG POPULATIONS OF THE EURASIAN TREE SPARROW (*PASSER MONTANUS*)

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ABSTRACT.—Eurasian Tree Sparrow (*Passer montanus*) populations, established by introductions outside of the native range, provide a unique opportunity to assess the relationship of morphometric and genetic change in a new environment. No statistically significant morphometric-genetic relationships were found among six populations of *P. montanus* when we (1) correlated morphometric size with heterozygosity; and (2) estimated degree of population differentiation using morphometric and genetic distance measures. Factors influencing both genetic and morphometric differentiation include the founding events and the ecological changes associated with them. *Received 21 Oct. 1986, accepted 1 May 1987.*

The relationship between genetically and ecophenotypically influenced morphometric variation is unknown in most studies. The degree of genetic-morphometric relationship may be clarified in part by examining the association or correlation of genetic characters, such as heterozygosity, with phenotypic states such as size (e.g., Wheat et al. 1974, bass [*Micropterus* sp.]; Singh and Zouros 1978, American oysters [*Crassostrea virginica*]; King 1985, herring [*Clupea harengus*]; Wooten and Smith 1985, mammals; see also Mitton and Grant 1984) or variation (e.g., Eanes 1978, monarch butterflies [*Danaus plexipus*]; Mitton 1978, killifish [*Fundulus heteroclitus*]; King 1985, herring; Fleischer et al. 1983, House Sparrows [*Passer domesticus*]). Other investigators (e.g., Zink 1982, Lindenfelser 1984, Van Wagner and Baker 1986) used multivariate methods (e.g., distance measures between populations) to examine the extent to which the genome and phenotype are similarly influenced. Two hypotheses attempt to explain observed genetic-morphometric relationships: (1) heterozygous lineages show superior growth rates, obtain greater size, and have buffered developmental processes, resulting in little morphological variation (heterosis [Lerner 1954]); and (2) increased environmental heterogeneity causes maintenance of high levels of genetic variation (e.g., Mayr 1954).

The Eurasian Tree Sparrow (*Passer montanus*) has been introduced

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extralimitally several times, for example, from West Germany to North America in 1870, and from China to Australia in 1863 (Long 1981). As a consequence of these introductions, this species has encountered a variety of new genetic (St. Louis and Barlow, in press) and environmental (Barlow 1973, 1980) influences. Factors influencing the genetic structure of the introduced North American population of *P. montanus* have included the general impact of the founding event, mutation, and stochastic processes such as genetic drift (St. Louis and Barlow, in press). Possible selective pressures on the genotypes, however, cannot be excluded as forces controlling the population's genetic structure. Differences in mensural characters between North American and ancestral German populations were attributed to the founding event and differential ecological conditions (Barlow 1973, 1980; Thompson 1983).

We studied relationships between genetic and morphometric variation and covariation among six populations of *P. montanus* by: (1) relating heterozygosity measures with morphometric "size" and (2) assessing the degree of population differentiation using morphometric and genetic distance measures to delineate causal factors influencing genotypic and, in particular, phenotypic structure of *P. montanus* populations.

METHODS

Samples from the North American population of *Passer montanus* were obtained between 1983 and 1985 at three locales in west-central Illinois (Woodson, Morgan County: N = 24, adult males [am] = 5, adult females [af] = 7; Naples, Scott County: N = 17, am = 4, af = 5; and White Hall, Greene County: N = 52, am = 15, af = 24) ca 40–50 km apart. Specimens of the ancestral European population came from Karlshrule, West Germany (N = 30, am = 10, af = 8), ca 50 km from Ludwigsburg where earlier samples studied by Barlow (1980) were obtained. The above samples were compared with each other and with Australian (N = 15, am = 8, af = 5) and Swedish (N = 25, am = 5, af = 9) specimens. Birds were collected from winter flocks with mist nets. Specimens were preserved in dry ice to minimize degradation of tissue enzymes. Skin-skeleton specimens were subsequently prepared at the Royal Ontario Museum in Toronto. Birds with skulls completely ossified were classified as adults (Nero 1951).

Horizontal starch gel electrophoresis of all *P. montanus* collected, used to measure the genetic structure of the populations, is described in St. Louis and Barlow (in press). Thirty-nine presumptive gene loci were resolved. Sixteen skeletal measurements (see Table 1) used by Johnston and Selander (1971) in studies of House Sparrow variation and by Barlow (1980) and Thompson (1983) on *P. montanus* were taken on the adult *P. montanus* using dial calipers accurate to 0.05 mm. A 17th variable (premaxilla length 2, measured from the posterior edge of the nasal to the anterior tip of the premaxilla) corresponding to Barlow's (1980) premaxilla length, was used for comparative purposes.

Principal component analysis (PCA) (Cooley and Lohnes 1971), based on a correlation matrix, was performed on the standardized means (mean = 0, SD = 1) of the raw data for the morphometric characters of each population for each sex to identify sets of characters that best described the variation among populations.

Taxonomic distances (Sneath and Sokal 1973) were computed from the standardized

TABLE 1

THE FIRST THREE PRINCIPAL COMPONENTS EXTRACTED FROM THE CORRELATION MATRIX AMONG MEANS OF SIX POPULATIONS OF *PASSER MONTANUS* FOR THE MALE AND FEMALE MORPHOMETRICS

	Males			Females		
Character	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
Premaxilla length 1	0.286	0.243	−0.009	0.191	0.304	0.094
Narial width	0.110	0.341	−0.081	−0.128	0.306	−0.390
Skull width	0.320	−0.062	0.170	0.305	−0.152	0.045
Skull length	0.236	0.252	0.299	0.170	0.317	0.279
Dentary length	0.156	0.354	−0.088	0.003	0.404	−0.087
Mandible length	0.311	0.199	−0.069	0.105	0.326	−0.280
Coracoid length	0.289	−0.245	−0.025	0.336	0.055	0.042
Sternum length	0.228	−0.282	−0.084	0.296	−0.199	0.043
Keel length	0.246	−0.214	−0.061	0.314	−0.514	0.073
Sternum length	0.036	−0.221	0.592	0.087	−0.057	0.685
Humerus length	0.315	−0.178	0.085	0.330	0.034	−0.159
Ulna length	0.290	0.113	0.360	0.306	0.170	−0.100
Femur length	0.215	−0.233	−0.337	0.307	−0.128	−0.218
Femur width	0.233	0.232	−0.327	−0.008	0.395	0.159
Tibiotarsus length	0.246	−0.222	−0.346	0.317	0.015	−0.216
Tarsometatarsus length	0.196	−0.279	0.121	0.324	−0.069	−0.111
Premaxilla length 2	0.217	0.279	0.095	0.074	0.379	−0.167
Eigenvalue	7.47	6.25	1.70	8.60	6.00	1.82
% Variation	44.0	36.8	10.0	50.6	35.3	10.7
Cumulative	44.0	80.8	90.8	50.6	85.7	96.6

means of the skeletal characters between populations for each sex using TAXON from the numerical taxonomic system of multivariate statistical programs, NTSYS (Rohlf et al. 1982). Through use of the unweighted pair-group method with arithmetic averages (UPGMA) (Sneath and Sokal 1973), a phenogram was obtained using TAXON from the taxonomic distances. Cophenetic correlation values were calculated for each phenogram to measure distortion between the original distance matrix and the phenogram.

Ordinations of the populations were obtained using nonmetric multidimensional scaling (Kruskal 1964a, b) (with MDSCALE from NTSYS [Rohlf et al. 1982]) on the taxonomic distances for each sex to establish interrelationships of the populations not indicated in a cluster diagram, and to compare with the ordination obtained from the genetic data (see St. Louis and Barlow, in press). A transformation on the taxonomic distances (using GOWER [Gower 1968] from NTSYS [Rohlf et al. 1982]) yielded a Q matrix (Gower 1968) of the populations which was used as initial input to multidimensional scaling. Goodness-of-fit of distances in the ordination to the monotonic function of the original distances was measured by calculation of stress values. A minimum spanning tree demonstrated proximity of populations in multidimensional space (Sneath and Sokal 1973).

Rogers' (1972) genetic distances, calculated from the electrophoretic data in St. Louis and

Barlow (in press), and taxonomic distances were compared using permutation tests (Dietz 1983) to determine covariation of genetic and morphometric data. Kendall's tau statistic was calculated from permutation tests using a Fortran program provided by Dietz (1983).

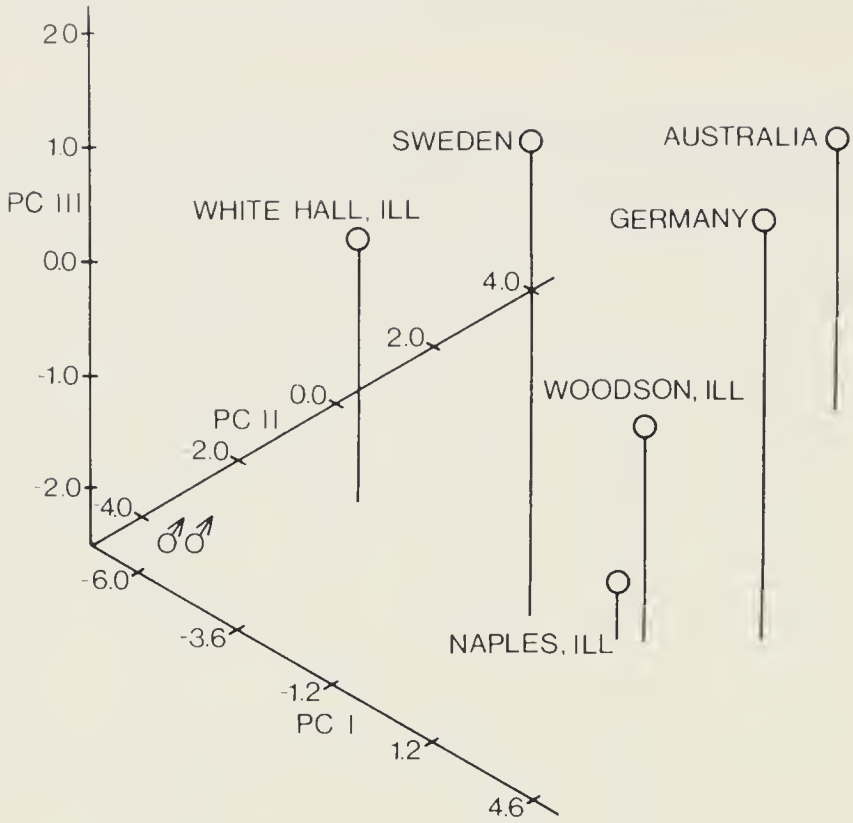
Spearman correlation coefficients on ranked means (Sokal and Rohlf 1969) were computed to assess the relationship (termed developmental homeostasis by Lerner [1954]; see also Zink et al. [1985] for review) between individual heterozygosity and individual size. Individual heterozygosity was calculated as the number of heterozygous loci per individual. The mean PC 1 or size value for individuals, determined a posteriori to PCA, was calculated for each heterozygosity value. PC 1 values were obtained from PCA for individual adults for each sex. Spearman coefficients on ranked means were also computed to assess the relationship between (termed genetic homeostasis [Lerner 1954; see also Zink et al. 1985]) population heterozygosity and mean morphometric size in the population. Population heterozygosity (direct count) values were obtained from St. Louis and Barlow (in press). Because there was no difference in allelic frequencies, age classes and the sexes were not separated. Size was determined a posteriori from scores of each population for each sex on PC 1, a size-related factor.

Spearman correlation coefficients on ranked means were computed to evaluate the relationship between mean morphometric size in the population (PC 1 scores) for each sex and average monthly and annual temperature (°C) and precipitation (mm). Temperature and precipitation data were obtained from Wernstedt (1972). Climatic variables for the periods July–December and January–June for North America and Europe were compared with corresponding January–June and July–December values for Australia.

Using climatic data obtained from U.S. Department of Commerce records, we calculated average monthly temperatures (°C) and precipitation (mm) for Jacksonville, Illinois (ca 10 to 50 km from the various Illinois collecting sites) to determine if any differences in local weather among North American sites occurred between 1982 and 1983 (two years prior to specimen acquisition at Woodson and Naples) and 1983 and 1984 (two years prior to sampling at White Hall).

RESULTS

The first three factors obtained from PCA accounted for 90.8% and 96.6% of the variation in male and female mensural characters respectively (Table 1). PC 1 accounted for 44% of the variation in males and was interpreted as representing overall size because all characters except sternal depth had positive loadings of similar value. No patterns of variation emerged that separated the introduced from the ancestral populations (Fig. 1). PC 2 in males was interpreted as reflecting shape because most body and appendage characters had negative loadings relative to head characters, with loadings, other than in skull width, showing similar values. PC 2 accounted for 36.8% of the variation. Along PC 2 for males, Australian specimens were distinct from other populations (Fig. 1). PC 3, which accounted for 10% of the variation, is more difficult to explain in general terms than PC 1 and PC 2. Sternal depth loaded highest, followed by leg characters. Skull length also loaded high on PC 3. PC 3 separated the German and Swedish populations from the others (Fig. 1). PC 1 in females, which accounted for 50.6% of the variation, was also



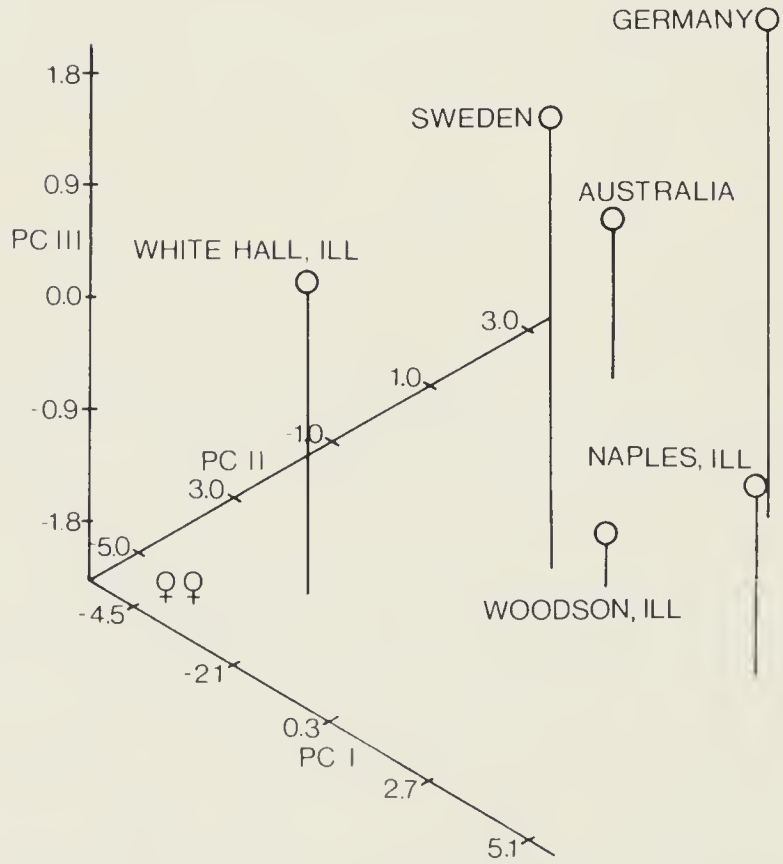


FIG. 1. Three dimensional principal component ordinations of skeletal characters of six populations of *Passer montanus* for males and females.

TABLE 2

TAXONOMIC DISTANCES BETWEEN POPULATIONS OF *PASSER MONTANUS* CALCULATED FOR MALE (ABOVE DIAGONAL) AND FEMALE (BELOW DIAGONAL) SKELETAL CHARACTERS

Population	1	2	3	4	5	6
Australia (1)		1.582	1.662	1.662	1.829	1.614
Germany (2)	1.418		0.985	1.101	1.956	0.887
Naples (3)	2.142	1.207		1.039	1.591	0.717
Sweden (4)	1.392	0.935	1.255		1.272	0.877
White Hall (5)	1.688	1.811	1.921	0.987		1.648
Woodson (6)	1.473	1.140	0.995	0.818	1.277	

size related. Length of sternum, keel and appendages had the highest loadings. Sternal depth, however, had a low positive value. As in the males, no patterns of variation in female characters were found that separated introduced from ancestral populations (Fig. 1). Head and bill characters (other than skull width) and femur width had high positive loadings on PC 2. PC 2 accounted for 35.3% of the variation in females. Sternal length and depth, keel length, femur length, and tarsometatarsus length had negative loadings that were lower than the values for head characters. Again, no pattern of variation emerged that distinguished the introduced from the ancestral populations (Fig. 1). PC 3 accounted for 10.7% of the variation. In males, PC 3 was more difficult to interpret than PC 1 and PC 2; sternal depth loaded highest. PC 3 for females separated the German and Swedish birds form the other samples.

Phenograms constructed from the taxonomic distances for each sex (Table 2) differed from each other in that the Woodson population clustered closest to the Naples and Swedish population in male and female clusters, respectively (Fig. 2).

A minimum stress of 0.005 or less ("excellent fit" [Kruskal 1964a]) was achieved with two dimensions for each sex and therefore was used to interpret the relationships of the populations (Fig. 3). The Australian males and females were most distant from other samples in their respective ordination figures. Swedish birds fell between White Hall and Woodson, with Naples closest to Woodson. The German and Australian populations had different positions in male and female ordinations. The German population was closest to Woodson and to Sweden in the ordinations of males and females respectively. The Australian population was closest to German and Swedish populations in the male and female ordinations respectively.

No significant similarity in distances between the populations was found

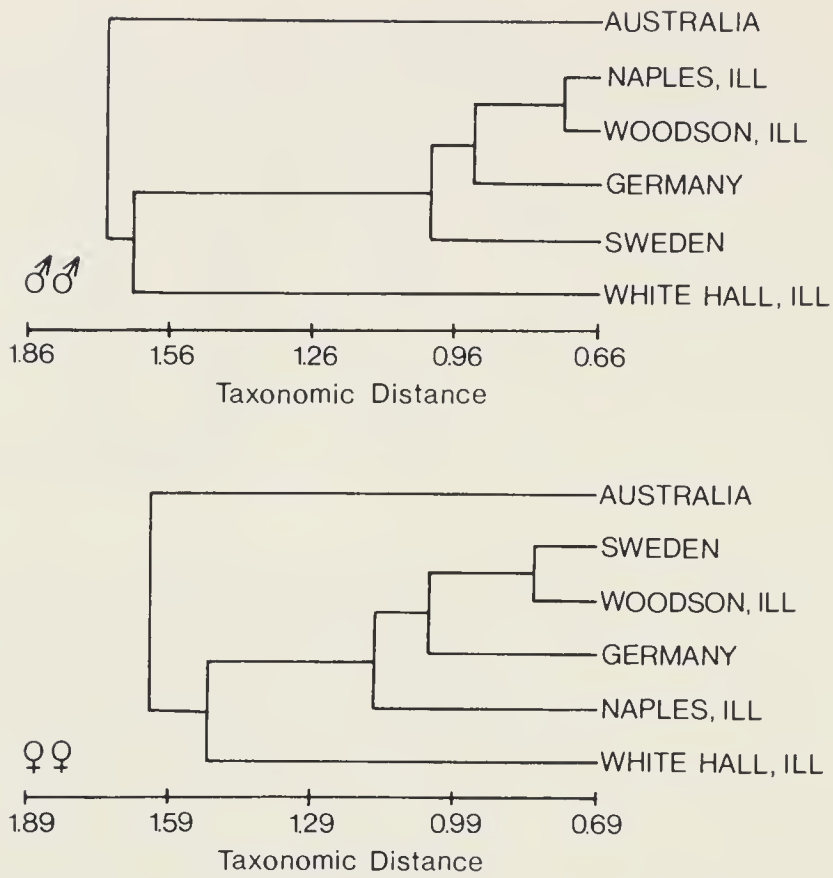


FIG. 2. UPGMA phenograms derived from the taxonomic distances among six populations of *Passer montanus* for the male and female skeletal morphometrics. The cophenetic correlation values were 0.928 and 0.710 for the male and female cluster analyses, respectively.

for male morphometric-genetic or female morphometric-genetic comparisons using the Kendall's tau statistic at the $P \leq 0.05$ level.

There was no significant relationship between mean individual size and individual heterozygosity in males ($r_s = 0.286$, $P = 0.53$) or females ($r_s = -0.107$, $P = 0.82$) (Fig. 4). There was also no significant relationship between population heterozygosity and population size in both males ($r_s = 0.714$, $P = 0.111$) and females ($r_s = 0.714$, $P = 0.111$) (Fig. 5).

No climatic variables were significantly correlated with PC 1 scores in males or females.

DISCUSSION

Genetic-morphometric relationships.—Phenotypic skeletal characters are influenced by both genetic structure of individuals and the ecological factors imposed upon the individuals during postembryonic development (Atchley et al. 1981, James 1983). Although size is partially heritable and controlled by many loci, both nutritional intake (e.g., Ricklefs 1968) and temperature (Gould and Johnston 1972) may affect the maximum po-

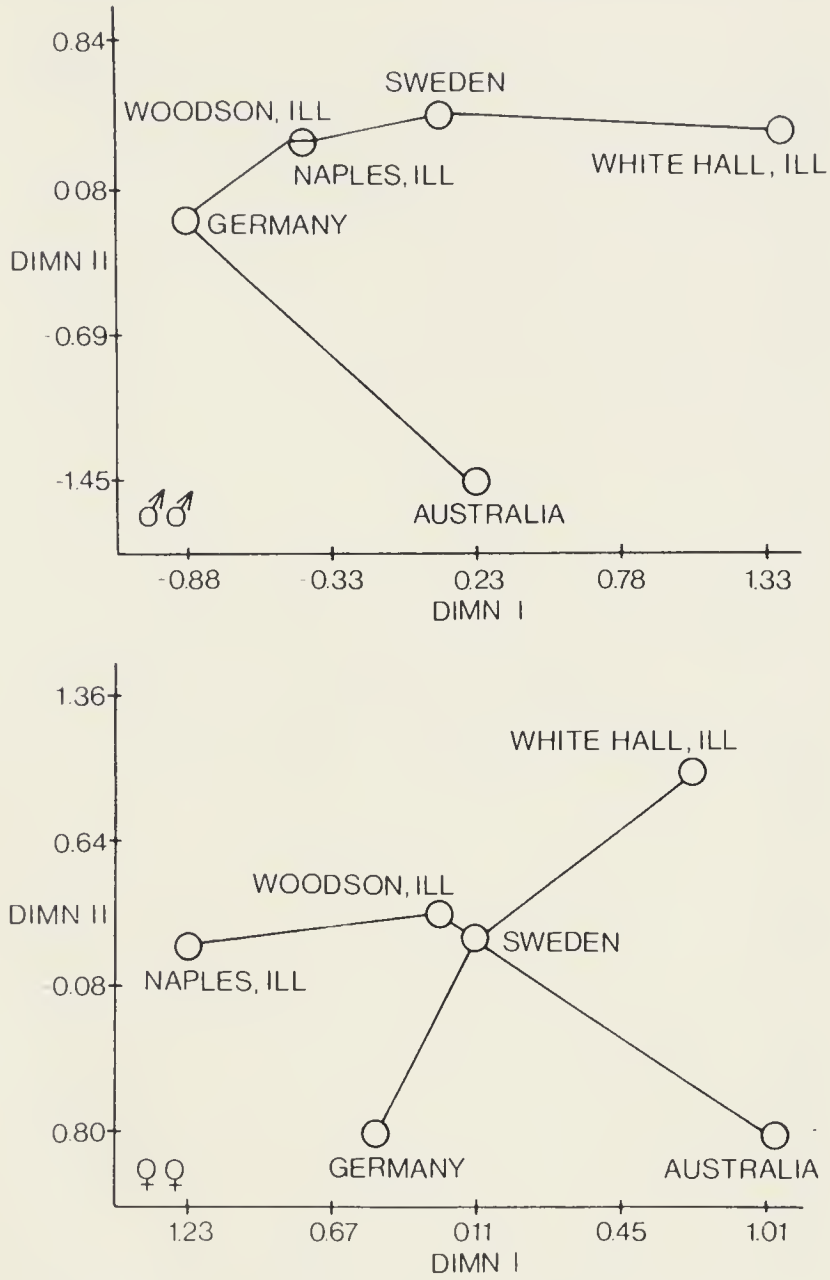


FIG. 3. Two dimensional ordinations from multidimensional scaling on the taxonomic distances among six populations of *Passer montanus* for the male and female skeletal morphometrics. Populations were joined using a minimum spanning tree (see text).

tential size reached by an individual. For the enzymes examined in electrophoretic studies, the proportion of heterozygous loci observed is assumed to be representative of the total genome (Barrowclough 1983). Morphometric differences between two populations, however, might not be reflected in allozyme loci that comprise only a portion of the genome (Wilson et al. 1977, Lewontin 1984). In the present study we found no significant relationship between either male or female genetic and morphometric comparison to support hypotheses regarding genetic-morpho-

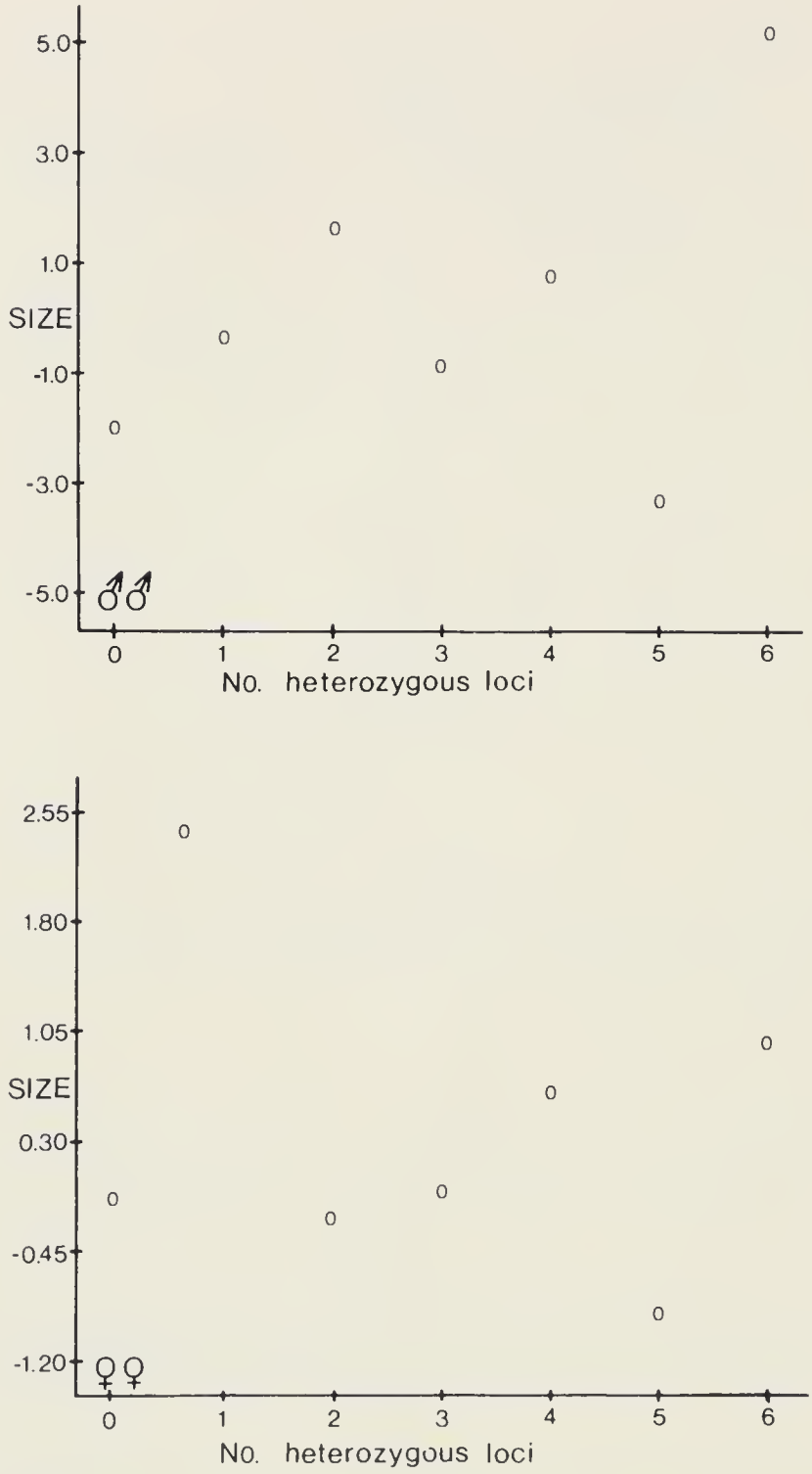


FIG. 4. Plot of number of heterozygous loci vs mean individual size for male and female *Passer montanus*.

metric covariation. St. Louis and Barlow (in press) previously attributed factors influencing genetic makeup of populations of *P. montanus* examined here to mutation, genetic drift, effective population size, and possibly unknown selective factors.

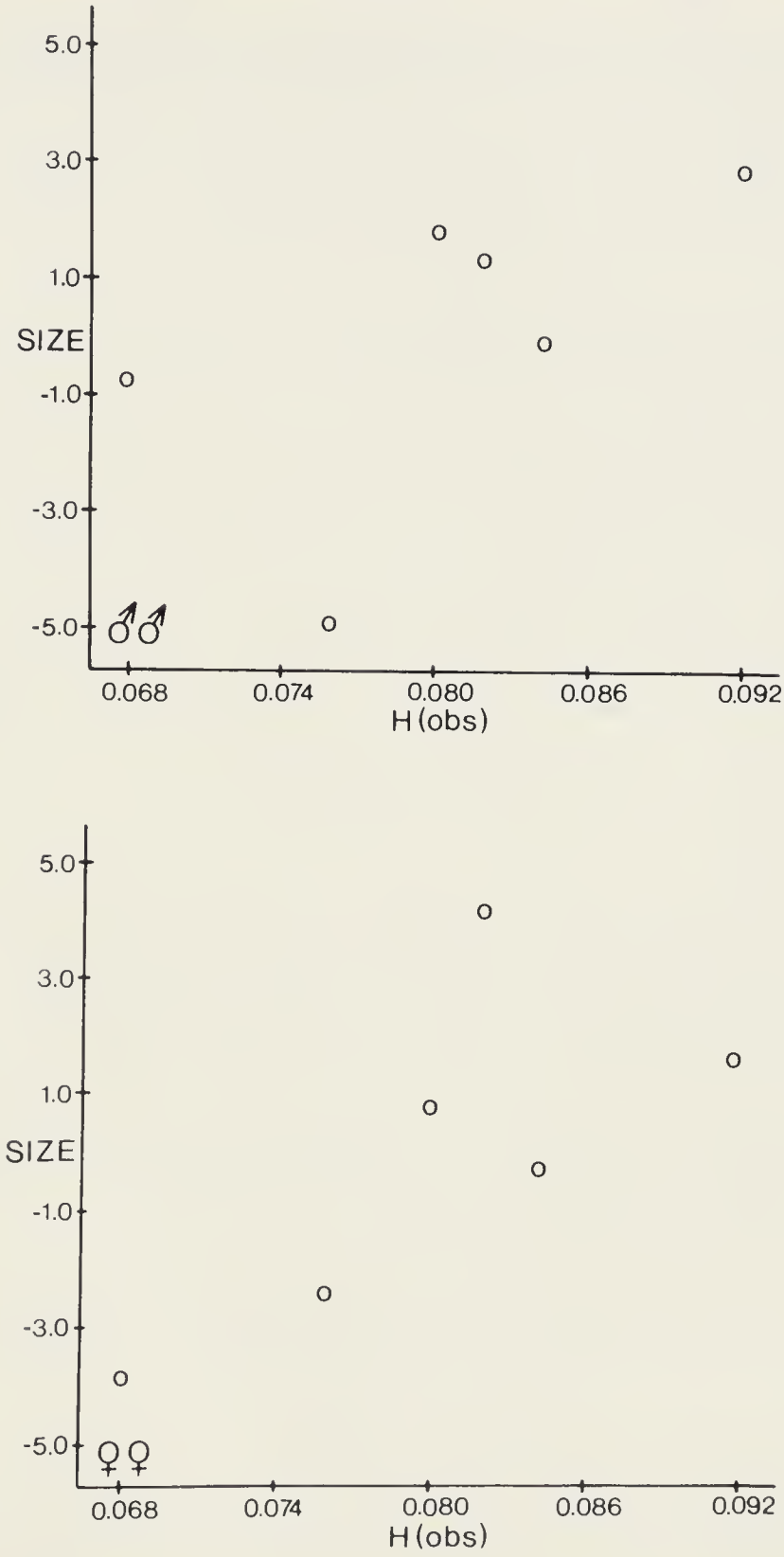


FIG. 5. Plot of observed heterozygosity vs mean population size of male and female *Passer montanus*.

Morphometric differentiation.—Differences in both sexes in bill and head characters between the German and North American populations of *P. montanus* were attributed to resource use by Barlow (1980) and Thompson (1983). Because a portion of the variation among populations of *P. montanus* is related to head and bill characters (PC 2) in males and females, it is thought that foraging-related differences occur across all the populations. PC 2 in males separated the Australian population from other samples. In the present study, variation in leg characters in male *P. montanus* only separated the Australian populations from the other five. Australian males had shorter and thicker legs than did males from the other populations. Because the Australian population inhabits the warmest climate of those encountered in this study, short legs with a large core area would not be expected in terms of thermoregulatory adaptations. Perhaps leg size difference of the Australian birds reflects difference in perching habits (Barlow 1980) or an unknown ancestral character state in the Chinese population. The shape component of female morphology (PC 2) indicated higher variation in head characters than in leg characters, and thus trends in females did not closely resemble those in Australian males. The differences in sternal depth between the North American and Australian and the German populations described by PC 3 may be a result of differential annual migration patterns and muscle developement (Barlow 1980).

Overall size, as explained by PC 1, showed no pattern of divergence among the populations corresponding to the known history of *P. montanus*. Variation in size, as reflected in the ordination of the North American populations in both PCA and two dimensional scaling, is partially accounted for by the differences seen between the smaller White Hall specimens and the other two North American populations, Woodson and Naples. Woodson and Naples were sampled a year earlier than White Hall, and overall size differences might be attributable to interannual variation in environmental conditions.

Influences on size.—Environmental factors are believed to be one influence on overall size in avian species (e.g., James 1970, 1983; Johnston and Fleischer 1981). We found no correlation, however, between average size in the populations and average climatic conditions for their respective regions. Temporally localized weather conditions, such as severe winter storms, are known to influence survival of certain House Sparrow phenotypes (Johnston et al. 1971, Rising 1973, Fleischer and Johnston 1982). In the above cases, in severe winters, large males survive, as do medium and small sized females (Johnston et al. 1971, Johnston and Fleischer 1981). In the present study winters prior to sampling at Woodson and Naples were colder for a longer period of time than winters prior to

sampling at White Hall. January snowfall as measured at Jacksonville was, on average, higher in 1982–83 than in 1983–84. Therefore it cannot be ruled out that ordination patterns of the North American populations of *P. montanus* in part are attributable to localized climatic conditions, such that the larger male Woodson and Naples birds suggest a preponderance of large size classes in severe winters, and smaller White Hall females reflect survival by them in milder winters.

Conclusions.—We believe that selective forces acting on the sexes separately and in concert, along with founder-induced ecological differences, such as food availability, account for approximately half of the morphometric variation seen across all populations in this study. Variation in size may be explained in terms of selective pressure from microenvironmental (e.g., severe climatic conditions) sources. Lack of correspondence, however, between genetic and morphometric data does not preclude a lack of genetic constraint on overall size or individual characters. Skeletal characters covary, and therefore are thought to be genetically related to some degree. The magnitude of any genetic influence cannot be assessed within the present study.

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VALUE OF SUBURBAN HABITATS TO DESERT RIPARIAN BIRDS

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ABSTRACT.—Bird populations were monitored over 20 consecutive months in suburban Tempe, Arizona, to assess the value of this artificial habitat for native riparian bird species. Of 104 species detected, 60 were transient migrants, 25 were permanent or summer residents that probably bred locally, and 19 were winter residents. Total density varied from 1423 to 3237 birds/40 ha; four nonriparian residents (Rock Dove [*Columba livia*], Inca Dove [*Columbina inca*], European Starling [*Sturnus vulgaris*], House Sparrow [*Passer domesticus*]) comprised from 52% to 72% of the total each month. Compared with nearby native riparian habitats (cottonwood-willow and mesquite), the suburban plots appeared to support significantly higher total bird densities in every month. Ten native species occurred in significantly higher density on the suburban transects than in outlying riparian habitats in at least one season. Overall, 53% of the riparian breeding species, and 85% of the winter residents also occurred in suburban Tempe. Absence of other riparian species from the suburban sites may be attributed either to interference by abundant, urban-adapted species or an inability to exploit nonnative tree species. Other suburban sites containing native willows and cottonwoods support populations of several obligate riparian species not found in Tempe. We suggest that well-vegetated suburban habitats have much potential in mitigating against the rapid loss of native riparian vegetation in the Southwest. *Received 8 Jan. 1987, accepted 7 May 1987.*

Urban and other artificial environments have been viewed as natural experiments in which the response of native bird communities to drastic habitat alterations can be investigated (Emlen 1974). Insights into the origin and organization of the urban avifauna of North America have come from studies in Illinois (Graber and Graber 1963), Massachusetts (Walcott 1974), Ohio (Beissinger and Osborne 1982), Arizona (Emlen 1974), Washington (Gavareski 1976), and British Columbia (Lancaster and Rees 1979). The uniformity of conclusions from these diverse regions is striking: urbanized habitats can support high densities of breeding birds, but are dominated numerically by a few nonnative and nonmigratory generalists. Comparison of present-day urban sites with nearby natural habitats has shown that native breeding species will persist in or recolonize areas that either retain some character of the natural vegetation or provide substitutes for specific habitat requirements, such as shrub cover or nest

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cavities (Linehan et al. 1967, Gavareski 1976, Beissinger and Osborne 1982).

In the southwestern United States, many native bird species are closely associated with desert riparian forests and particularly sensitive to habitat loss (Carothers et al. 1974, Johnson et al. 1977). Water-use practices and large scale clearing of natural vegetation for agriculture have resulted in a drastic reduction in riparian habitats and the bird species that depend on them. When urbanization follows land clearing, vegetation cover may increase again through planting. Preliminary data from the Colorado River Valley (Anderson and Ohmart 1976, 1977) and the Phoenix region (S. B. Terrill, pers. obs.) indicated that suburban areas may support many native species, including some considered sensitive to riparian habitat loss. Our goals in this study were to: (1) quantify avian populations throughout the year in a well-vegetated suburb; (2) compare these population trends with those in nearby riparian habitats; and (3) evaluate the potential value of these man-made habitats to native bird species in the arid southwest.

STUDY AREA AND METHODS

We established two 0.8 km transects in a relatively well-vegetated section of Tempe, Arizona (elev. 355 m). One was along a quiet suburban street (Ash St., between 13th St. and University Ave.), bordered on both sides by landscaped front yards in which mature plantings included pecan (*Carya illinoensis*), mulberry (*Morus alba*), palms (*Washingtonia robusta* and *W. tilifera*), ash (*Fraxinus pennsylvanica*), and firethorn (*Pyracantha fortuneana*). A few native cottonwoods (*Populus fremontii*), palo verdes (*Cercidium* spp.), and cacti were scattered along the transect. The second transect was along an unpaved lane paralleling a dirt-lined irrigation ditch, two blocks south of Apache Blvd. between McAllister and Mill avenues. Eight mature willow trees (*Salix goodingi*) grew along the ditch, which contained water during 10% of the census visits. This transect was bordered in part by several open dirt or grassy lots, a small orchard of pecans, several citrus trees (*Citrus* spp.), figs (*Ficus cariaca*), and two large honey mesquite trees (*Prosopis glandulosa*). The remainder was adjacent to fenced back yards with variable vegctation cover. We chose these transects not as representative of suburban Tempe, but rather to indicate the potential value of more densely vegetated urban areas to birds.

Each transect was censused by the variable-width line transect method (Emlen 1971, 1977) during three mornings each month from September 1979 through June 1981. The study encompassed two complete winters and two breeding seasons. Approximately 85% of the censuses were conducted by the authors, with the remainder by five additional observers. Densities of all bird species were computed separately for each census based on the distribution of detections among lateral strips 15–30 m in width. We took the maximum density of detections in successively wider strips and extrapolated this to number/40 ha (see Anderson et al. 1977, Engel-Wilson et al. 1981). Estimates from the six censuses (for both transects) were averaged to yield one monthly density value for each bird species.

We compared these densities with those from cottonwood-willow and mesquite-dominated habitats near the confluence of the Salt and Verde rivers, approximately 20 km northeast of Tempe, surveyed by Stamp and Ohmart (1976). The census technique and

density calculations were identical to our own, and Terrill censused extensively in both studies, thus facilitating our comparison. Average seasonal density estimates for each habitat were compared using a Student's *t*-test for small, unequal sample sizes (Sokal and Rohlf 1969). Although the riparian and suburban habitats were censused in different years, our extensive visits to these sites over a 5-year period did not detect any major changes in avifaunal composition. Year-to-year fluctuations in abundance are to be expected; therefore, our statistical comparisons must be treated with caution. The qualitative conclusions from these comparisons, however, are not diminished by these weaknesses.

Because of the irregular seasonal status of many southwestern birds, we use breeding resident, rather than "summer" resident, to denote species that migrate to the region in spring to breed, and nonbreeding resident to denote those that occur for part of the year but do not breed. Similarly, we denote April to June as the breeding season and November to January as the season when birds are most clearly wintering. These designations follow Phillips et al. (1964) and Monson and Phillips (1981).

RESULTS

We detected a total of 104 species on the two transects, 60 of which occurred only as transients or rare visitors. Among the 44 permanent or seasonal residents (Table 1), four were classified as nonriparian by Ohmart and Anderson (1982). These are the exotic Rock Dove (scientific names are in Table 1), European Starling, and House Sparrow, as well as the native Inca Dove, the spread of which into the southwestern United States closely paralleled human settlement (Phillips et al. 1964, Rea 1983). The latter three species each attained minimum year-round densities of >300 birds/40 ha and peaked at between 500 and 900 birds/40 ha in some months.

Of the remaining native species, the Northern Mockingbird and House Finch were the most abundant year-round, usually exceeding 100 birds/40 ha. White-winged and Mourning doves were also abundant in spring and summer. Other native species that attained relatively high and stable densities in the suburban sites included Gila Woodpecker, Verdin, Abert's Towhee, and Northern Cardinal. Black-chinned Hummingbird was common in summer, and Northern (Red-shafted) Flicker, Yellow-rumped Warbler, and White-crowned Sparrow were relatively common in winter.

The number of permanent resident species (including nonriparian) remained nearly constant (13–15) throughout the study period (Fig. 1). The number of breeding residents peaked at seven in June–August 1980 and nine in May 1981, whereas nonbreeding residents peaked at 14 species in November 1979 and 17 in January 1981. Transient species outnumbered all other groups in September of both years (21–22 species), with smaller peaks in April–May.

Total density throughout the study period ranged from 1423 birds/40 ha in November 1979 to 3237 birds/40 ha in April 1981 (Fig. 2). Four nonriparian species accounted for 52–72% of the total density during all months. Densities of both riparian and nonriparian species were highest

TABLE 1

DENSITY (BIRDS/40 HA) OF BREEDING AND WINTERING RESIDENTS IN SUBURBAN TEMPE, ARIZONA, COMPARED WITH NATIVE RIPARIAN HABITATS

Species	Riparian affinity[a]	April–June		November–January	
		Density	Status[b]	Density	Status[b]
Sharp-shinned Hawk (*Accipiter striatus*)	F			3 ± 3	P
American Kestrel (*Falco sparverius*)	F			3 ± 2	P
Gambel's Quail (*Callipepla gambelii*)	F		– –		– –
Rock Dove (*Columba livia*)	N	70 ± 19[c]	+ +	88 ± 16	+ +
White-winged Dove (*Zenaida asiatica*)	F	113 ± 68	0		
Mourning Dove (*Z. macroura*)	F	196 ± 59	+	30 ± 32	+
Inca Dove (*Columbina inca*)	N	405 ± 40	+ +	387 ± 130	+ +
Yellow-billed Cuckoo (*Coccyzus americanus*)	O		– –		
Greater Roadrunner (*Geococcyx californianus*)	F	V[b]	– –		
Black-chinned Hummingbird (*Archilochus alexandri*)	F	33 ± 7	0		
Anna's Hummingbird (*Calypte anna*)	F	8 ± 8	0	12 ± 8	+ +
Gila Woodpecker (*Melanerpes uropygialis*)	F	22 ± 8	–	23 ± 3	0
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	F			3 ± 2	0
Ladder-backed Woodpecker (*Picoides scalaris*)	F		– –		
Northern Flicker (*Colaptes auratus*)	F		– –	21 ± 5	+
Ash-throated Flycatcher (*Myiarchus cinerascens*)	F	2 ± 2	–		
Brown-crested Flycatcher (*M. tyrannulus*)	F	V	– –		
Western Kingbird (*Tyrannus verticalis*)	F	2 ± 5	P		
Cliff Swallow (*Hirundo pyrrhonota*)	F	3 ± 6	P		
Verdin (*Auriparus flaviceps*)	F	53 ± 16	+	33 ± 6	+
Cactus Wren (*Campylorhynchus brunneicapillus*)	F	7 ± 7	0	1 ± 1	0

TABLE 1
CONTINUED

Species	Riparian affinity[a]	April–June		November–January	
		Density	Status[b]	Density	Status[b]
Bewick's Wren (*Thryomanes bewickii*)	O		– –	3 ± 2	0
House Wren (*Troglodytes aedon*)	F			2 ± 1	P
Ruby-crowned Kinglet (*Regulus calendula*)	F			15 ± 10	–
Blue-gray Gnatcatcher (*Polioptila caerulea*)	F			2	P
Black-tailed Gnatcatcher (*P. melanura*)	F		– –		– –
Western Bluebird (*Sialia mexicana*)	F				– –
Hermit Thrush (*Catharus guttatus*)	F			3 ± 2	P
American Robin (*Turdus migratorius*)	F			5 ± 8	0
Northern Mockingbird (*Mimus polyglottos*)	F	196 ± 37	+	83 ± 31	+ +
Curve-billed Thrasher (*Toxostoma curvirostre*)	F	12 ± 7	+	7 ± 2	+
Crissal Thrasher (*T. dorsale*)	O		– –		
Cedar Waxwing (*Bombycilla cedrorum*)	F			2	P
Phainopepla (*Phainopepla nitens*)	F		– –		– –
Loggerhead Shrike (*Lanius ludovicianus*)	F		– –	3 ± 3	0
European Starling (*Sturnus vulgaris*)	N	316 ± 97	+	305 ± 117	+
Bell's Vireo (*Vireo bellii*)	O		– –		
Solitary Vireo (*V. solitarius*)	F			1 ± 2	P
Orange-crowned Warbler (*Vermivora celata*)	F			8 ± 5	P
Lucy's Warbler (*V. luciae*)	O	1 ± 1	–		
Yellow Warbler (*Dendroica petechia*)	O	V	– –		
Yellow-rumped Warbler (*D. coronata*)	F			79 ± 31	+

TABLE 1
CONTINUED

Species	Riparian affinity[a]	April–June		November–January	
		Density	Status[b]	Density	Status[b]
Yellow-breasted Chat (*Icteria virens*)	O		– –		
Summer Tanager (*Piranga rubra*)	O	V	– –		
Northern Cardinal (*Cardinalis cardinalis*)	F	19 ± 6	0	11 ± 4	+
Blue Grosbeak (*Guiraca caerulea*)	O		– –		
Green-tailed Towhee (*Pipilo chlorurus*)	F			V	– –
Abert's Towhee (*P. aberti*)	O	49 ± 18	0	23 ± 11	–
Lincoln's Sparrow (*Melospiza lincolnii*)	F			3 ± 2	P
White-crowned Sparrow (*Zonotrichia leucophrys*)	F			23 ± 23	0
Dark-eyed Junco (*Junco hyemalis*)	F			2 ± 2	P
Red-winged Blackbird (*Agelaius phoeniceus*)	F			18 ± 20	P
Great-tailed Grackle (*Quiscalus mexicanus*)	F	53 ± 23	+ +	14 ± 4	+ +
Bronzed Cowbird (*Molothrus aeneus*)	F	24 ± 7	+ +		
Brown-headed Cowbird (*M. ater*)	F	48 ± 32	0		
Hooded Oriole (*Icterus cucullatus*)	O	3 ± 4	0		
Northern Oriole (*I. galbula*)	O	3 ± 4	–		
House Finch (*Carpodacus mexicanus*)	F	266 ± 57	+	126 ± 49	+
Lesser Goldfinch (*Carduelis psaltria*)	O	V	– –		
House Sparrow (*Passer domesticus*)	N	789 ± 98	+ +	406 ± 117	+ +

[a] From Ohmart and Anderson (1982); O = Obligate riparian, F = Facultative riparian, N = nonriparian.

[b] Comparison with highest density in either cottonwood-willow or mesquite habitat 20 km NE of Tempe (data from Stamp and Ohmart 1976). + + = occurred only in suburban; + = significantly higher density in suburban (*t*-test, $P < 0.05$); – = significantly lower in suburban (*t*-test, $P < 0.05$); – – = recorded on riparian but not on suburban transects, 0 = no significant difference between suburban and native habitats; P = not recorded by Stamp and Ohmart but known to occur in small numbers in riparian habitats (pers. obs.); V = visitor only to suburban habitat.

[c] Mean density ± SD.

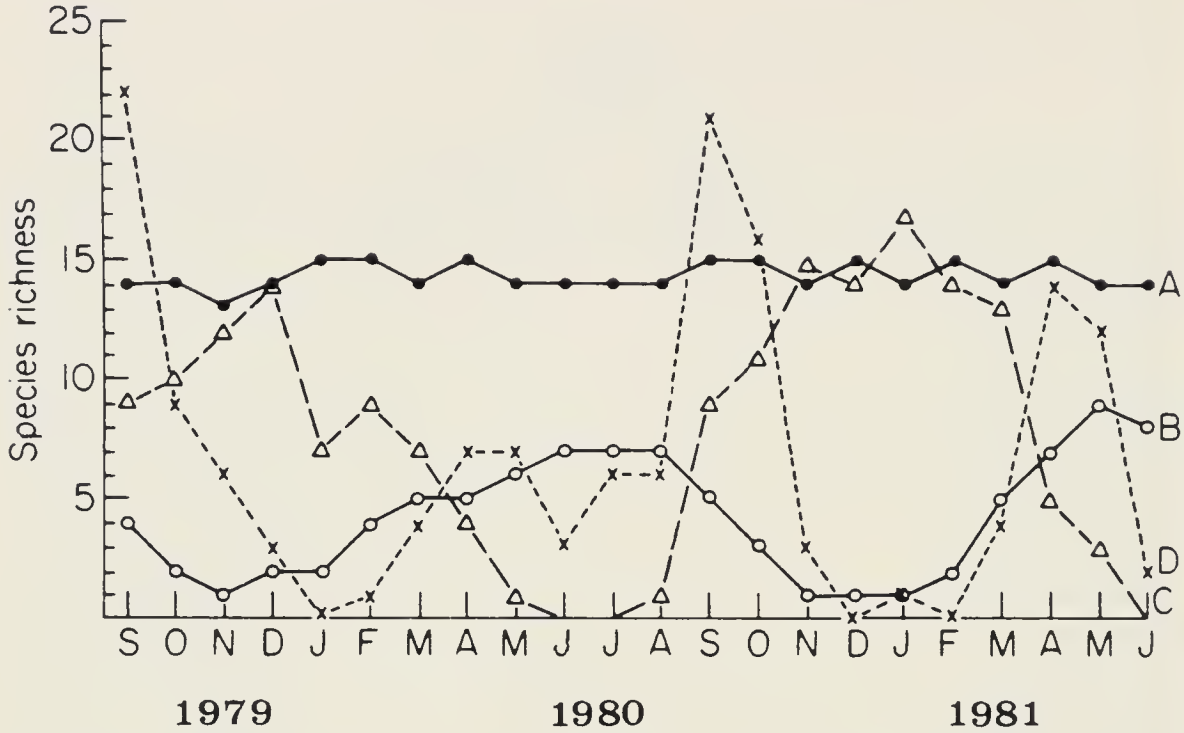

FIG. 1. Monthly bird species richness in suburban Tempe, Arizona: A—Permanent residents; B—Breeding residents; C—Nonbreeding residents; D—Transients.

during the spring breeding season and fell sharply in late fall and early winter, essentially paralleling population trends in mature cottonwood/willow habitat (Stamp and Ohmart 1976). Postbreeding flocks of Inca Doves, starlings, and House Sparrows caused a second peak for nonriparian species each September.

The largest proportion of individuals on the plots at all times were permanent residents (Fig. 3). In the two successive years, permanent resident density dropped 49–54% from September to the winter low, then roughly doubled again by the following April. Breeding resident density rose gradually through late winter and spring, while density of nonbreeding residents was dropping gradually from a November-December peak. Average monthly density of transients was relatively low with a maximum of 111 birds/40 ha recorded in September 1979; counts on single days, however, produced estimates as high as 260 birds/40 ha.

Comparison with riparian habitats.—Because our primary purpose for quantifying the suburban bird community was to make comparisons with nearby riparian communities, we drew heavily on similar data gathered in cottonwood and mesquite habitats by Stamp and Ohmart (1976). During the April–June breeding season, 43 nontransient species were detected on either riparian or suburban transects (Table 1). Of these, the Rock Dove, Inca Dove, Great-tailed Grackle, Bronzed Cowbird, and House Sparrow may be considered "suburban" species that did not breed in the

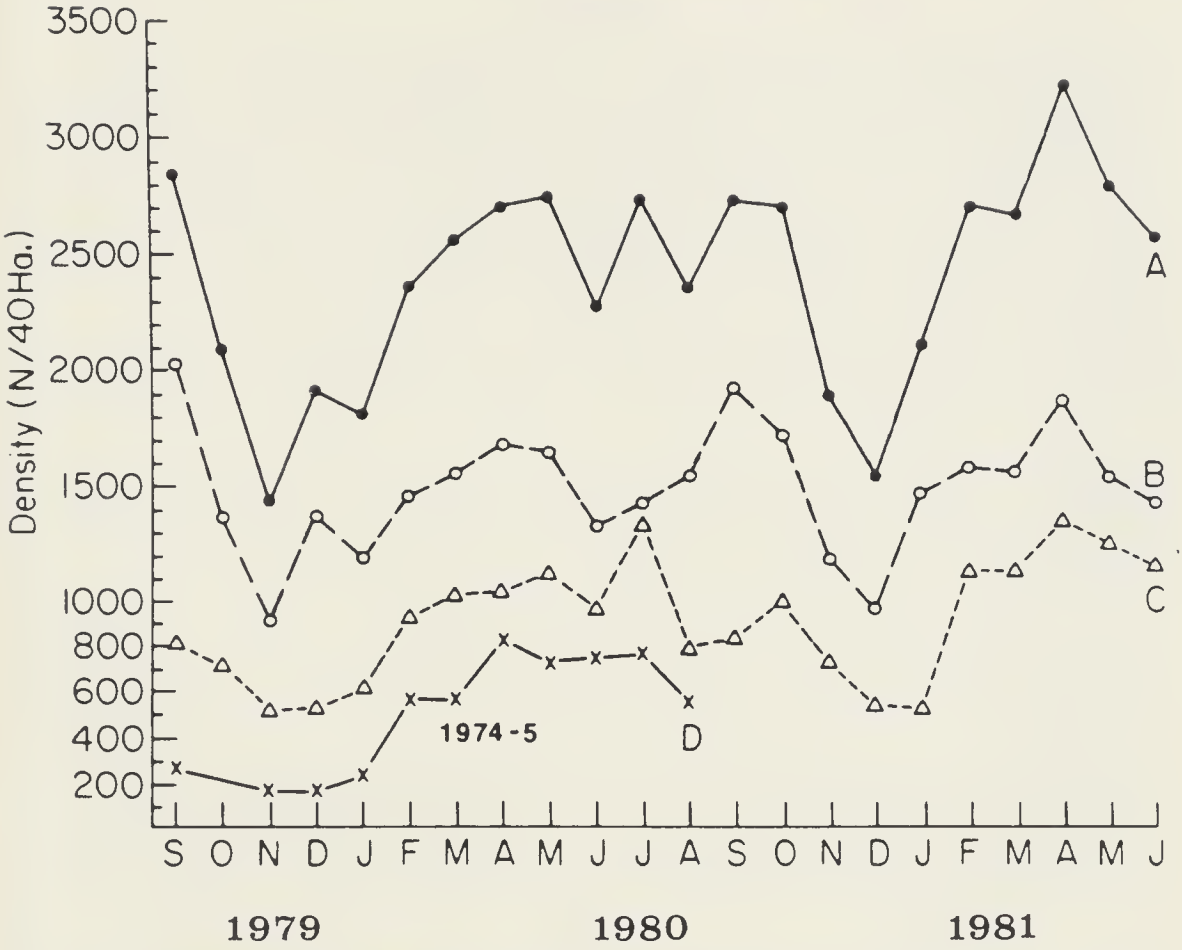

FIG. 2. Monthly bird density in suburban Tempe, Arizona: A—Total density; B—Non-riparian species (Rock Dove, Inca Dove, European Starling, House Sparrow); C—Native riparian species; D—Total density in cottonwood-willow habitat 20 km NE of Tempe (data from Stamp and Ohmart 1976).

native habitats. European Starlings, although much more abundant in town, did nest in some riparian areas. Other native species (Mourning Dove, Anna's Hummingbird, Verdin, Northern Mockingbird, Curve-billed Thrasher, Brown-headed Cowbird, House Finch) occurred in significantly higher densities in the suburban community (Table 1) and thus, appear to be well adapted to that environment. Densities of six additional species (Table 1) were not significantly different between suburban and riparian habitats. Gila Woodpecker, Ash-throated Flycatcher, Lucy's Warbler, and Northern Oriole occurred in Tempe, but in significantly lower densities than in riparian habitat; of these, only the woodpecker regularly nested in town. Finally, 17 riparian species were absent from Tempe, including obligate riparian birds such as Yellow-billed Cuckoo, Bell's Vireo, Yellow Warbler, and Summer Tanager. Overall, 53% of the species detected on riparian transects also occurred on the suburban plots.

In winter (November–January), 39 species were found on either riparian

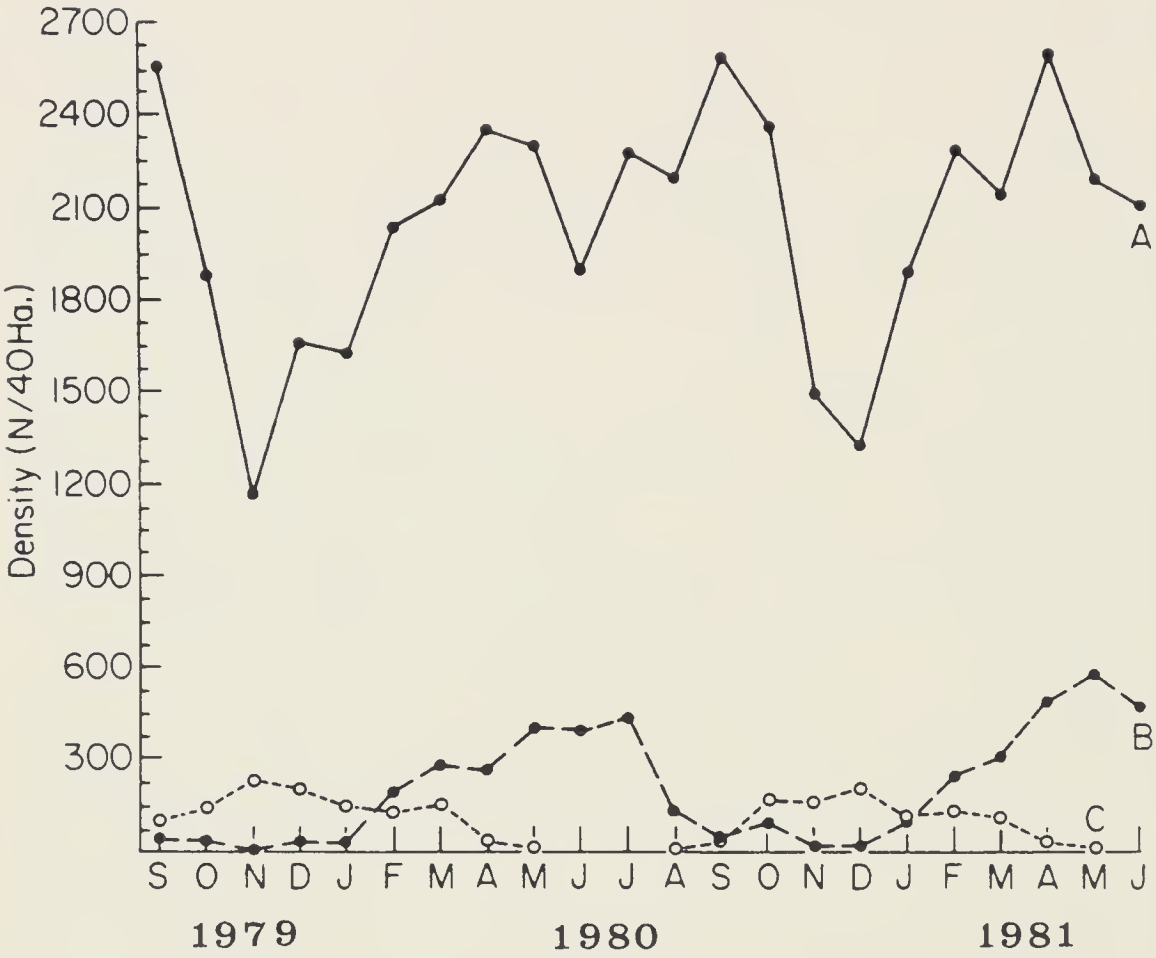

FIG. 3. Monthly density of permanent and seasonal residents in suburban Tempe, Arizona: A—Permanent residents; B—Breeding residents; C—Nonbreeding residents.

or suburban transects (Table 1). Species considered "suburban" were similar to those above except that in addition, Anna's Hummingbird and Northern Mockingbird occurred only in Tempe at this season. Species occurring in significantly higher densities in Tempe were also similar to those in the breeding season with the addition of winter residents, Northern (Red-shafted) Flicker and Yellow-rumped Warbler. Yellow-bellied Sapsucker, Cactus Wren, Bewick's Wren, Loggerhead Shrike, and White-crowned Sparrow were found in roughly equal densities in the two areas, whereas Ruby-crowned Kinglets and Abert's Towhees were in significantly lower numbers on the suburban plots. In addition, 11 uncommon species were found wintering in Tempe, which although not detected on riparian transects, are known to occur in small numbers in these areas (pers. obs.). The only riparian species absent from Tempe were Gambel's Quail, Western Bluebird, Black-tailed Gnatcatcher, Phainopepla, and Green-tailed Towhee. Thus, roughly 85% of the wintering riparian species used the suburban habitat to some extent at that season.

DISCUSSION

Suburban community composition.—The presence of abundant food, surface water, and a benign climate undoubtedly combine to sustain the extremely high density of birds noted in Tempe. Similarly, Emlen (1974) noted a 26-fold increase in summer density from desert to urban habitats at Tucson, Arizona, largely accounted for by introduced species. In spite of the very large urban-species component of the Tempe community, native nonurban species attained higher total density there year-round than in even the most productive native habitat, cottonwood-willow (Fig. 2).

Urban studies in other regions have identified specific features of these habitats that limit their bird assemblages. In general, permanent residents have responded more positively to unnatural aspects such as artificial food sources, than have migratory breeders (Linehan et al. 1967, Lancaster and Rees 1979). For example, Walcott (1974) documented a large shift in species dominance from summer residents to permanent residents over a century (1860–1964) in Cambridge, Massachusetts, as did Aldrich and Coffin (1980) after 37 years in Virginia. Similarly, we found both native and introduced permanent residents to far outnumber seasonal visitors throughout the year in Tempe. In fragmented forest tracts of eastern North America, migratory species also have fared less well than have residents (Whitcomb et al. 1981), due in part to higher rates of nest predation, particularly near suburban areas (Wilcove 1985).

The importance of increased surface water due to human activities was noted by Emlen (1974) at Tucson and by Davies (1977) in arid Australia, but was not found to be significant in more humid regions (e.g., Lancaster and Rees 1979). Food supply is also generally enhanced in man-made habitats, particularly for ground-foraging and granivorous species. Migratory, foliage-gleaning insectivores have often been the most reluctant to colonize urban habitats, responding when they do to natural features such as native plant species, vegetation structure, and the presence of woodlots (Linehan et al. 1967, Lancaster and Rees 1979, Beissinger and Osborne 1982). Understanding what combination of factors limits the occurrence of this latter group of birds in southwestern urban environments is critical to the problem of making these areas more attractive to native riparian specialists.

First, it is of interest to consider the recency with which typically urban bird species have enjoyed success in the Southwest, as chronicled by Phillips et al. (1964), Monson and Phillips (1981), and Rea (1983). All were unrecorded in Arizona prior to 1900, with the most recent invaders to the Phoenix area being the Great-tailed Grackle (1950s) and Anna's Hummingbird (1960s). It is evident, therefore, that what we now consider

to be a major component of suburban bird communities in the region constitutes a relatively recent addition to the local avifauna. The impact of these population increases on other local species, and particularly on potential colonists from native habitats, is also very recent. It is likely that abundant starlings, House Sparrows, and cowbirds disrupt the breeding of many cavity- and small open-nesting species, although direct evidence from our study sites is lacking.

Besides possible interference by urban-adapted species, there is evidence that vegetation composition may affect the presence of certain specialized riparian birds. Several migratory, summer-breeding species, including Yellow-billed Cuckoo, Yellow Warbler, Yellow-breasted Chat, and Summer Tanager, are highly dependent on mature cottonwood-willow stands in the Southwest (Hunter 1984, Ohmart and Anderson, unpublished data). That the absence of these and other species from suburban habitat in Tempe may be attributable to the scarcity of native tree species among suburban plantings is further supported by data from Willow Valley estates near Bullhead City, Arizona (Anderson and Ohmart 1977). This mobile home community is planted almost entirely with native willows and cottonwoods, and the surrounding land has largely been cleared for agriculture. About half of the riparian breeding bird species absent from Tempe are represented here, including virtually all the cavity-nesters, as well as the Yellow Warbler and Summer Tanager. In addition, qualitative observations in Tempe show that the few native willows, cottonwoods, and mesquite trees were heavily used for foraging and nesting, whereas disproportionately few birds were observed in exotic mulberries or eucalyptus. Thus, many riparian bird species can be attracted to human habitations by planting native tree species.

Value of suburban habitats to riparian birds.—In addition to the permanent and seasonal residents discussed above, we noted over 50 species of transients on the Tempe transects. These included virtually all regularly occurring terrestrial migrants of the region, as well as species such as Blackpoll Warbler (*Dendroica striata*), Canada Warbler (*Wilsonia canadensis*), and Scarlet Tanager (*Piranga olivaceus*), that are extremely rare in Arizona. The attractiveness of natural and artificial desert oases to migrants is well known. Urban areas can provide such an oasis in regions where virtually all natural vegetation has been removed and therefore may be important to many southwestern migrant species.

In summary, we have shown that roughly half of the local riparian breeding avifauna use habitat in suburban Tempe, and we suggest that more species might be attracted if certain native trees were planted. In winter, an even greater proportion of local native species probably find the suburban habitat to be suitable. Finally, the planted urban vegetation

appears to be relatively important for migrants. Thus, these areas may not be complete barriers to species dispersing along southwestern river valleys, as suggested by Rea (1983). The presence of humans or their structures does not seem to inhibit the occurrence of many species.

Considering the present emphasis on preservation and management of riparian ecosystems, the potential for managing suburban areas for native birds should not be overlooked. Managers of parks, recreation sites, and private residences can enhance the value of these areas to birds by incorporating selected native trees in their plantings. Unfortunately, we have rarely seen this done. Finally, large-scale revegetation of previously cleared land has been shown to be efficient and effective for reestablishing native bird communities (Anderson et al. 1978). Such efforts may be instrumental in maintaining populations of specialized or declining bird species in regions where little riparian vegetation remains.

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Wilson Bull., 99(4), 1987, pp. 655–662

FREQUENCY AND TIMING OF SECOND BROODS IN WOOD DUCKS

Robert A. Kennamer and Gary R. Hepp[1]

Abstract.—Occurrence of second broods in Wood Ducks (*Aix sponsa*) was studied during 1982–1986. Successful second nests comprised 7.6% (21 of 275) of all nesting attempts in which females were identified and 9.6% (21 of 219) of successful nestings. Length of the nesting season averaged 157 days. Average initiation dates of the first and second nests of double-brooded females were 14 February and 16 May, respectively. Mean interval between hatching of first nests and initiation of second nests was 47 days. Minimum age of females that produced two broods was 2.3 years. Mean egg mass, clutch size, clutch mass, and body mass of females were greater for first nests than for second nests. We compared first nests of double-brooded females with nests of single-brooded females that initiated nests during the same time period (20 January–4 March). There were no differences in mean egg mass, clutch size, clutch mass, body mass, and age between single-brooded and double-brooded females. Females producing one brood, however, lost a greater percentage of body mass during incubation than did double-brooded females. *Received 4 Nov. 1986, accepted 10 Apr. 1987.*

Reports of Wood Ducks (*Aix sponsa*) having two broods in a single nesting season are common (Odom 1970, Fredrickson and Hansen 1983). Little, however, is known about the factors that contribute to an individual's ability to rear two broods. Other species of North American anatids do not usually nest successfully more than once in a breeding season, and some species rarely renest if the first nest is destroyed (Bellrose 1980). In Wood Ducks and other species of ducks, it seems likely that length of the breeding season influences the probability of producing a second brood. Fredrickson and Hansen (1983), for example, reported that Wood Duck populations nesting at northern latitudes have second broods much less often than do populations at southern latitudes where the breeding season is longer. Drobney (1982) hypothesized that production of second broods by female Wood Ducks also may be related to their use of exogenous protein during laying and incubation, which conserves endogenous protein and may shorten the time needed to reach prebreeding condition again. In addition, annual variations in climate (e.g., precipitation and temperature), and its influence on the acquisition and maintenance of nutrient reserves, may affect the frequency of second broods at the population level.

In this paper, we report the frequency and timing of second broods in a southern Wood Duck population during five breeding seasons. Mean

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egg mass, clutch size, and clutch mass are compared between first and second nests. We also relate female age, length of the breeding season, and weight loss during incubation to the probability of producing a second brood.

STUDY AREA AND METHODS

The study was conducted on the Department of Energy's Savannah River Plant (SRP) in west-central South Carolina (33.1°N, 81.3°W). Wood Duck nest boxes were erected on the SRP during the mid-1970s (Fendley 1978). In 1982–1986 nest boxes generally were checked weekly during the nesting season (January–July). We used data on second broods from this 5-year period. Length of the nesting season was the number of days between initiation of the first nest and hatching of the last nest.

Wood Duck nests were determined to be the result of one (normal nest) or more (dump nest) females. Identification of dump nests was based on at least one of the following criteria: (1) egg deposition rate exceeded one egg per day, (2) viable nonterm eggs were present at hatching, and (3) clutch size was ≥17 eggs (Morse and Wight 1969). Length (L) and breadth (B) of all eggs were measured to the nearest 0.1 mm with vernier calipers. L, B, and fresh mass (M) of 105 Wood Duck eggs were used to predict fresh egg mass from external egg measurements:

$$M = 0.993 + 0.00054\ (LB^2),$$

$P < 0.0001$, $R^2 = 0.97$. Egg mass estimates from this equation were used to calculate mean egg mass and clutch mass of normal nests.

Each year most breeding females were captured in nest boxes and banded with U.S. Fish and Wildlife Service leg bands. We also web-tagged day-old ducklings (Haramis and Nice 1980), and the return of web-tagged females to breed provided a sample of known-age individuals. Our sample of female Wood Ducks consisted of (1) known-age individuals, (2) females that nested and were banded in previous years but were not web-tagged (i.e., exact ages were not known), and (3) females that were neither banded nor web-tagged at time of capture. Nesting females that were not banded or web-tagged were called 1-year-old birds. Mean age of females, therefore, is a minimum estimate. In 1986, mass of females was recorded to the nearest 5 g with 1000-g Pesola spring scales during early (≤9 days) and late (≥26 days) incubation.

Wilcoxon's signed-ranks test was used to compare characteristics of first and second nests of double-brooded females (Sokal and Rohlf 1981). Comparisons of single-brooded and double-brooded females were based on rank-transformed data (Conover and Iman 1981). Other analyses were made using the Statistical Analysis System (SAS Institute Inc. 1985). Sample means are presented ±1 SE. We used 2-tailed tests, and statistical significance levels were set at the 0.10 probability level.

RESULTS

Second brood frequency and timing.—In 1982–1986, Wood Ducks initiated 429 nests; of these, 275 (64.1%) nesting females were captured. A total of 219 (51.1%) nests was successful in producing at least one duckling, and we captured the female in 210 (95.9%) successful nests. Hens with second broods comprised 7.6% (21 of 275) of all nests in which females were identified and 9.6% (21 of 219) of successful nests. One female had

TABLE 1

NESTING SEASON LENGTH AND THE OCCURRENCE OF SECOND BROODS IN WOOD DUCKS ON THE SAVANNAH RIVER PLANT, 1982–86

	Length of nesting season[a]	Successful nests	No. of females captured/No. of nesting attempts	No. of double-brooded females
1982	145	34	34/67	1[b] (2.9[c], 2.9[d])
1983	172	46	58/99	4 (8.7, 6.9)
1984	156	48	65/101	5 (10.4, 7.7)
1985	134	30	36/57	0
1986	179	61	82/105	11 (18.0, 13.4)
All years	157 ± 8.3[e]			
Totals		219	275/429	21 (9.6, 7.6)

[a] Length of the nesting season is the number of days from initiation of the first nest to hatching of the last nest.
[b] Number of double-brooded females.
[c] Percentage of successful nests that were successful second nests.
[d] Percentage of all nests in which females were captured that were successful second nests.
[e] $\bar{x}$ ± SE.

second broods in two different years. In 1986, two additional females produced and incubated second clutches, but these nests were abandoned before the eggs hatched.

Length of the nesting season on the SRP averaged 157 days (Table 1). Second broods were not produced during the shortest nesting season (1985), but occurred most frequently in the longest season (1986) (Table 1). Mean initiation date of first nests for female Wood Ducks that produced two broods was 14 February ± 3 days (N = 21; range = 20 January–4 March). Mean earliest initiation date for all females during the 5-year period was only 10 days earlier. Average initiation date of second nests for females producing two broods was 16 May ± 4 days (N = 21; range = 9 April–13 June). The mean interval between hatching of first nests and initiation of second nests was 47 ± 4 days (N = 21; range = 19–92 days).

Characteristics of first and second nests.—Double-brooded females were known-age individuals (N = 4), females that nested and were banded in previous years but were not web-tagged (N = 11), and females that were neither banded nor web-tagged at the time of capture (N = 5). Mean minimum age of all females that produced two broods was 2.3 ± 0.3 years (N = 20; range = 1–5). Four known-age females averaged 2.3 years, and one of these individuals was a yearling.

A comparison of double-brooded females' first and second nests showed that mean egg mass, clutch size, and clutch mass were greater ($P < 0.05$) for first nests (Table 2). Body mass of females in early incubation also was greater for first nests than for second nests (Table 2). Females, how-

TABLE 2
MATCHED-PAIRS COMPARISON OF THE FIRST AND SECOND NESTS OF DOUBLE-BROODED WOOD DUCKS, 1982–1986[a]

Variable	N	First nest[b]	Second nest[b]	*P*
Mean egg mass (g)	9	43.9	41.7	<0.01
Clutch size	9	13.0	10.0	<0.01
Clutch mass (g)	9	610.5	412.3	<0.01
Female body mass (g)[c]	8	632.5	572.5	<0.01
Percent change in body mass during incubation	6	−6.5	−3.6	N.S.

[a] Wilcoxon's signed-ranks test.
[b] Median values.
[c] Body mass of female Wood Ducks in early incubation (≤9 days).

ever, lost a similar percentage of body mass during incubation of both nests (Table 2).

Comparisons of single-brooded and double-brooded females.—Females that produced one brood in 1986 and initiated nests in the same period (20 January–4 March) as females that produced two broods were compared to double-brooded females. Errors in determining nesting status (single-brooded vs double-brooded) of females in 1986 should have been small because all females that nested successfully in nest boxes were captured. Movement of females between nest boxes (first nest) and natural cavities (second nest) may have occurred; however, this movement should have been minimal due to the philopatric behavior of female Wood Ducks (Hepp et al. 1987). There were no differences ($P \geq 0.35$) in mean egg mass, clutch size, clutch mass, and female age between single- and double-brooded females (Table 3). Body mass of single- and double-brooded females also was the same at the start of incubation, but females that produced two broods lost a smaller percentage of body mass during incubation (Table 3).

DISCUSSION

Female Wood Ducks in this study produced second broods more frequently than Wood Ducks at higher latitudes (see review in Fredrickson and Hansen 1983). In general, length of the breeding season for birds in temperate regions is inversely related to latitude (Wynham 1986), and breeding season length may influence the production of second broods by Wood Ducks. For example, average duration of the nesting season for Wood Ducks in South Carolina (SRP) was 60 days longer than Grice and Rogers (1965) reported for Wood Ducks in Massachusetts (157 vs 97

TABLE 3
REPRODUCTIVE PARAMETERS OF SINGLE-BROODED AND DOUBLE-BROODED FEMALE WOOD DUCKS IN 1986[a]

Variable	Single-brooded female	Double-brooded female	t	df	P
Nest initiation date	16 Feb (2.4)[b]	9 Feb. (4.0)	1.0	10,10	0.35
Mean egg mass (g)	43.6 (1.0)	45.1 (1.0)	−0.8	5,5	0.45
Clutch size	13.3 (0.7)	13.5 (0.4)	−0.1	5,5	0.94
Clutch mass (g)	579.1 (24.7)	607.7 (14.0)	−0.8	5,5	0.45
Female body mass (g)[b]	610.0 (14.3)	617.5 (12.4)	−0.5	10,7	0.61
Percent change in body mass during incubation	−9.4 (1.0)	−4.3 (2.8)	−1.9	8,5	0.08
Female age	2.6 (0.4)	2.4 (0.5)	0.6	10,10	0.49

[a] Data are from first nesting attempts; t-tests are performed on rank-transformed data.
[b] $\bar{x} \pm$ SE.
[c] Body mass of female Wood Ducks in early incubation (≤9 days).

days), and approximately 10% of the females in South Carolina that nested successfully had second broods compared with <1% in Massachusetts. Average time between first and second nests in South Carolina was 47 days. The length of time that Wood Duck hens remain with broods during rearing can vary from 30 to 60 days (Grice and Rogers 1965, Ball et al. 1975, Hepp 1977). Time constraints may prohibit females nesting at high latitudes from successfully producing and rearing two broods, molting, and migrating from northern areas before winter.

Frequency of second broods varied annually in South Carolina, and it was related to differences in the timing and duration of the nesting seasons. Second broods were not produced during 1985 when nesting began relatively late and ended early (13 February–26 June; 134 days). Second broods occurred most frequently during 1986 when Wood Ducks nested early, and the nesting season was long (20 January–18 July; 179 days). Annual differences in nesting chronology and length of the breeding season can be caused by variation in the proximate factors that affect food availability (Perrins 1970). Nesting begins late for some prairie-nesting ducks during years of low spring temperatures and drought conditions that negatively affect the invertebrate food base of breeding females (Krapu et al. 1983, Afton 1984). Renesting by female Lesser Scaup (*Aythya affinis*) that have had first nests destroyed is also less frequent during dry years (Afton 1984). Lipid reserves of female Wood Ducks provide 88% of the lipid and energy requirements of an average-size clutch, while protein for eggs is obtained from exogenous sources (Drobney 1982). Female Wood Ducks may delay breeding until they develop a "threshold" level of lipid reserves

(sensu Alisauskas and Ankney 1985). Factors that affect development and maintenance of lipid reserves and acquisition of protein may influence time of nesting and length of the breeding season and thereby influence the occurrence of second broods at the population level. In South Carolina, when breeding conditions were good (i.e., nesting started early and ended late), approximately 18% of female Wood Ducks produced two broods. The ability to produce two broods in a season was not restricted to adult females.

Mean egg mass, clutch size, clutch mass, and body mass of double-brooded females were smaller for second nests than for first nests. Fredrickson and Hansen (1983) also reported that clutch size and female body mass of double-brooded Wood Ducks declined between the first and second nests. Clutch sizes of renesting ducks generally are smaller than first nests, and smaller clutches of Mallards (*Anas platyrhynchos*) are correlated with smaller lipid reserves of breeding females (Krapu 1981). Female ducks apparently do not establish lipid reserves prior to renesting, as they do for first nests, but depend on exogenous nutrients at the breeding site for egg production (Krapu 1981, F. Rohwer, pers. comm.). Dependence on exogenous sources for both the energy and nutrient demands of renesting attempts may limit clutch size and egg size (Krapu 1981). Hohman (1986) proposed that the nutrient status of breeding Ring-necked Ducks (*Aythya collaris*) varied annually and that smaller lipid reserves of prebreeding females caused a greater reliance on exogenous nutrients during reproduction, resulting in delayed breeding and reduced clutch size in some years. During second nests, body mass of double-brooded females was smaller than during first nests, and they produced smaller clutches and eggs. Smaller body mass of female Wood Ducks indicated that they may have had less lipid reserves at the beginning of second nests and, hence, were dependent more on exogenous nutrients for clutch development. Smaller clutch size and egg mass of Wood Duck second nests, therefore, simply may reflect reduced lipid reserves of females and a greater reliance by females on unpredictable exogenous nutrients for egg production, as reported in other species of waterfowl. Without experimental studies, however, we cannot rule out the possibility that seasonal reductions in clutch size were the result of ultimate (e.g., average amount of food available to the hen and young) rather than proximate factors as proposed by Batt and Prince (1979).

We found no differences in egg mass, clutch size, and clutch mass of first nests of double-brooded females and nests of single-brooded females that nested during the same period of time (20 January–4 March 1986). Female Wood Ducks that produced two broods, therefore, did not appear to expend less energy on first clutches than females that produced only

one brood. Age and body mass of single-brooded and double-brooded females also did not differ. Single-brooded females lost a greater percentage of body mass (9.4%) during incubation than double-brooded females (4.3%). Mass loss during incubation averaged 26.5 g for the first nest of double-brooded females and 57.3 g for females that produced one brood. For other species of waterfowl mass loss during incubation is greater (12–32% of initial body weight) than it is for Wood Ducks (see review in Gatti 1983). Drobney (1980, 1982) reported that female Wood Ducks had an average of 31 g of fat at the end of laying and used about 17 g during incubation; there was no loss of carcass protein during incubation. Assuming that females in this study started to incubate with similar levels of lipids, then single-brooded females depleted all lipid reserves and probably also used some endogenous protein to meet the energy costs of incubation. Lipid reserves of double-brooded females, however, were not exhausted during incubation of first nests. We suggest that high weight loss during incubation may affect the probability of producing a second brood in either of two ways: First, by depleting lipids and using some endogenous protein to help meet the energy demands of incubation, hens may need more time to replenish these reserves, thereby increasing the renesting interval and decreasing renesting ability. Second, nutritional status of birds is known to affect reproductive development (Huxley 1976, Ottinger 1983). Bluhm et al. (1983), for example, showed that environmental stressors can affect hormonal characteristics of Mallards, thereby blocking reproduction. Greater incubation weight loss of single-brooded female Wood Ducks may have been sufficiently stressful to depress gonadal function and terminate reproductive activity.

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EGG MASS, POSITION IN THE LAYING SEQUENCE, AND BROOD SIZE IN RELATION TO CANADA GOOSE REPRODUCTIVE SUCCESS

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ABSTRACT.—To better understand the effects of egg mass and position in the laying sequence on reproductive success of Canada Geese (*Branta canadensis*), I determined the fate of eggs, marked embryos near hatching, and recaptured goslings near fledging. Hatching success did not correlate with egg mass and position in the laying sequence. The probability of recapturing marked goslings near fledging was not associated with relative egg mass or position in the laying sequence. These results suggest that egg mass and position in the laying sequence have no short-term implications for the fitness of the chick produced. A reduced survival rate of goslings in larger broods in one year suggests that brood size could be a factor limiting clutch size in Canada Geese. *Received 17 Mar. 1986, accepted 16 Mar. 1987.*

Hatching and fledging success in Anserinae can be reduced by extrinsic (environmental) factors such as predation (Vermeer 1970, Cooper 1978), climate (Cooper 1978), and intraspecific competition (Ewaschuk and Boag 1972). Intrinsic factors such as egg size, egg quality, and position in the laying sequence have been shown to correlate with hatching and fledging success in some nidicolous species (Parsons 1970, Murton et al. 1974, Howe 1976, O'Connor 1979, Rofstad and Sandvik 1985) but in contrast, little is known regarding these factors for nidifugous species. Brood size also influences fledging success in some nidifugous species (Safriel 1975, Andersson and Eriksson 1982), but not in others (Heusmann 1972, Glasgow 1977, Clawson et al. 1979, Rohwer 1985).

Here, I examine the effects of egg size and position in the laying sequence on hatching and fledging success of Canada Geese (*Branta canadensis*). I address the following questions: (1) Are hatching and fledging success related to egg mass at laying and position in the laying sequence? (2) Does brood size at hatching correlate with brood size near fledging?

STUDY AREA AND METHODS

The study was carried out in 1983 and 1984 near Brooks, Alberta (50°35′N, 111°54′W). From late March to early May each year, I searched for nests daily at Gleddie Lake. In six other reservoirs nearby, I searched for nests every 2 to 4 days. Nearly all nests had 1 or 2 eggs when found, although some had 3. When more than 1 egg was found in a nest, the degree of staining of eggs was used to assess the order of laying (Cooper 1978). Subsequent

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visits to the nest allowed me to determine the position in the laying sequence of additional eggs. Upon discovery, each egg was weighed with a spring scale and its maximum length and breadth were measured with vernier calipers to the nearest 0.1 mm. I considered a clutch successful if at least 1 egg hatched. In each successful clutch, the fate of each egg was classified as successful, disappeared or preyed upon, broken, incubated but not hatched, deserted, or flooded. I considered an egg successful if a gosling emerged from the shell.

At Gleddie Lake, I marked individual members of most broods at the time the eggs were pipped, by tagging each embryo in the egg with a numbered web-tag (after Alliston 1975). I marked 171 goslings from 32 broods in 1983 and 151 from 29 in 1984. Banding drives were conducted 8 and 6 weeks after the peak of hatching in 1983 and 1984 respectively, to capture flightless adults and goslings. All goslings were examined for the presence of a web-tag.

In 1984 at other reservoirs, 44 clutches of 6 eggs with the completed laying sequence known were removed from their nests during the last week of incubation and placed in an incubator at the Brooks Wildlife Center.

I defined hatching success as the proportion of eggs surviving to the time of hatching that produced a chick (Cooper 1978, Koenig 1982). Brood size was defined as the number of goslings leaving the nest. Because most of the mortality of goslings occurs during the first 2 weeks of life (e.g., MacInnes et al. 1974, Zicus 1981), I considered the number of goslings reaching fledging age as the number recaptured.

The effect of position in the laying sequence and egg mass on hatching and fledging success were analyzed with 3-way contigency tables (Sokal and Rohlf 1981). The position in the laying sequence of each egg was classified as being either first, middle, or last laid. I also assigned each egg to two categories of sizes: small, if the fresh mass was below the mean value for both years of study (i.e., 163 g), or large, if equal or above this value. The significance of an interaction was tested by a test of partial association (Dixon et al. 1983). To control for sources of between year variation in the analysis of the relationship between the percentage of goslings recaptured per brood and mean egg mass, I standardized means of egg masses per clutch by subtracting from each mean egg mass the grand mean for the year it was taken.

RESULTS

Hatching success.—A total of 118 nests (67 in 1983; 51 in 1984) were discovered and followed through the hatching period at Gleddie Lake. Broken eggs in 7 nests that were not attributable to predation or strife between adjacent territorial pairs were not different in mass from the intact eggs of their clutch (Wilcoxon signed-ranks test; $T = 0.507$, $P > 0.30$). Thirty-three and 30 clutches were successful in 1983 and 1984, respectively. Because there were no differences between naturally and artificially incubated clutches in the proportion of unsuccessful eggs (G-test; $G = 0.961$, df = 2, $P > 0.50$), I combined these data to increase sample sizes. Hatching success was independent of the position in the laying sequence and the relative size of the egg (Table 1). Moreover, of successful clutches in which at least one fully incubated egg did not hatch (N = 33), the mean mass of these unhatched eggs was not different from the mean mass of successful eggs within the same clutch ($T = 0.90$, $P > 0.35$, N = 33).

TABLE 1
HATCHING OF EGGS IN RELATION TO THEIR POSITION IN THE LAYING SEQUENCE AND THEIR RELATIVE SIZE, 1983–1984

		Number		Partial association[a]			
Position	Size	Hatched	Unhatched	Effect	df	G	P
First	Below mean[b]	59	3	HSP[c]	2	4.81	0.071
First	Above mean	30	4	HS	1	0.63	0.320
Middle	Below mean	173	12	HP	2	1.86	0.355
Middle	Above mean	178	9	SP	2	13.00	0.002
Last	Below mean	60	3				
Last	Above mean	27	6				

[a] Interaction among variables.
[b] $\bar{x}$ = 163 g.
[c] Test of partial association of a 3-way contingency analysis, factors: H, hatching success; S, size of the egg; P, position in the laying sequence.

Fledging success.—There was no relationship between the size of a brood and its probability of disappearing in 1983 (Table 2). In 1983 mean egg mass of clutches in which at least one gosling was recaptured was smaller than that from clutches in which no goslings were recaptured (t-test; $t = 2.40$, df = 30, $P = 0.02$), but there was no difference in 1984 ($t = 1.27$, df = 27, $P = 0.22$). Among the 40% (13/32: 1983) and 34% (10/29: 1984) of broods in which no goslings were recaptured, a high percentage had probably moved overland to other areas or simply fledged and left the study area by the date of the banding drive (see Giroux 1980).

To reduce the bias created by departures of broods from the study area, the following analyses were performed on the set of data that includes only broods in which at least one gosling was recaptured. There was no significant correlation between age of the brood and percentage of goslings recaptured in both years of study (Spearman rank correlation, 1983, $r_s = -0.04$, $P = 0.86$, N = 19; 1984, $r_s = -0.16$, $P = 0.52$, N = 19). The probability of a gosling being recaptured was independent of its position in the laying sequence and the relative size of the egg from which it hatched (Table 3). Within each clutch, there was no difference between the mass of eggs from which recaptured and not recaptured goslings hatched both in 1983 ($t = 0.283$, $P > 0.75$, N = 19) and 1984 ($t = 0.440$, $P > 0.66$, N = 19). In addition, the percentage of goslings recaptured in a clutch was not related to standardized mean egg mass of the clutch (Fig. 1).

The effect of brood size on survival rates was investigated by comparing brood size at hatching with the number of goslings recaptured per brood. The number of goslings recaptured per brood was not statistically different among brood sizes in either year, nor in the 2 years combined (Table 4).

TABLE 2

NUMBER OF BROODS RECAPTURED AS A FUNCTION OF BROOD SIZE IN THE STUDY AREA, 1983–1984

Year		Brood size							G^a	df	P
		1	3	4	5	6	7	8			
1983	Recaptured	1		4	7	5	1	1	1.68	2	>0.25
	Not recaptured	1		5	2	4	1	0			
1984	Recaptured		2	6	4	5	2	0	1.16	2	>0.50
	Not recaptured		2	1	4	2	1	0			
1983–1984 combined	Recaptured	1	2	10	11	10	3	1	0.03	2	>0.97
	Not recaptured	0	2	6	6	6	2	0			

[a] Sizes of brood were grouped in 3 classes: ≤4 goslings; 5 goslings; ≥6 goslings.

To see whether larger broods lost proportionately more goslings than did smaller broods, I tested whether the slope of a regression line drawn through the logarithms of the number recaptured and the initial brood size differed from one (after Ricklefs et al. 1978). I found that larger broods lost proportionately more goslings than did smaller broods ($t = 2.69$, df = 17, $P = 0.02$) in 1984, but not in 1983 ($t = 1.77$, df = 17, $P = 0.09$).

DISCUSSION

Effect of egg mass on hatching and fledging success.—Egg mass does not correlate with hatching success for Canada Geese (this study), Lesser Snow Geese (*Chen caerulescens caerulescens*; Cargill 1979), Red Grouse (*Lagopus lagopus scoticus*; Moss et al. 1981), and Ring-billed Gulls (*Larus delawarensis*; Ryder 1975). Wang (1982) reported that unhatched eggs were 3.2 g lighter on average than hatched ones for Giant Canada Geese (*B. c. maxima*). He suggested that small females that were in poorer condition laid smaller eggs and left their nest more often exposing eggs to cold stress. In Mallards (*Anas platyrhynchos*), large incubated eggs were more resistant (higher % of them hatching) to prolonged exposure at 0°C than were small eggs (Batt and Cornwell 1972). Natural differences in mass of eggs of Canada Geese may be not large enough to affect hatching success significantly in years of normal weather.

Larger eggs produced larger chicks in Canada Geese (Leblanc 1986), Snow Geese (Ankney 1980), and Mallards (Rhymer 1982). Larger precocial chicks survived longer than smaller chicks in controlled experiments (Ankney 1980, Moss et al. 1981, Rhymer 1982). In a natural environment, Cole (1979) showed that in one year larger Snow Goose goslings survived better than did smaller ones. The following year, how-

TABLE 3

NUMBER OF GOSLINGS THAT WERE RECAPTURED AT PREFLEDGING IN RELATION TO THEIR POSITION IN THE LAYING SEQUENCE AND THEIR RELATIVE SIZE (DETERMINED BY EGG MASS AT LAYING), 1983–1984

Position	Size	Persistence		Partial association[a]			
		Recaptured	Not recaptured	Effect	df	*G*	*P*
First	Below mean[b]	8	12	PeSP[c]	2	3.59	0.166
First	Above mean	9	4	PeS	1	0.39	0.534
Middle	Below mean	25	18	PeP	2	2.99	0.225
Middle	Above mean	41	37	SP	2	10.42	0.006
Last	Below mean	6	14				
Last	Above mean	6	7				

[a] Interaction among variables.
[b] $\bar{x}$ = 163 g.
[c] Test of partial association of a 3-way contingency analysis, factors: Pe, persistence; S, size of the egg; P, position in the laying sequence.

ever, the pattern was reversed, with smaller chicks surviving better than larger ones. Other researchers have found no relationship between survival of the chick and egg size (Herring Gulls [*Larus argentatus*], Davies 1975; Kittiwakes [*Rissa tridactyla*], Barrett and Runde 1980; Great Skuas [*Catharacta skua*], Williams 1980; and Canada Geese, this study). Egg mass may influence survival in Canada Geese, but because the effect may be small, detecting it can be difficult (Rotenberry and Wiens 1985). As for hatching success, the effect of egg mass on fledging success may depend on the occurrence of infrequent, but severe, environmental conditions, and its importance may only be revealed during "bottle-neck" years.

Effect of position in the laying sequence on hatching and fledging success.—The first egg of a clutch had poorer hatching success than all other eggs in Giant Canada Geese (Cooper 1978, Wang 1982). Seven failed eggs were either the last laid or second last laid egg in the Hooded Crow (*Corvus corone*) (Rofstad and Sandvik 1985). The second and the third egg were more successful in producing young than the first or the fourth egg in the Shag (*Phalacrocorax aristotelis*) (Snow 1960). In these studies, however, the presence of a relationship between egg mass and position in the laying sequence precluded determining which one of these 2 factors was the most important. If egg quality is associated with position in the laying sequence, some eggs from particular positions may be more likely to fail. Parental protection may also differ among eggs of different positions because females are progressively more attentive to their nest during laying (Cooper 1978). These factors, however, did not seem to play an important role in

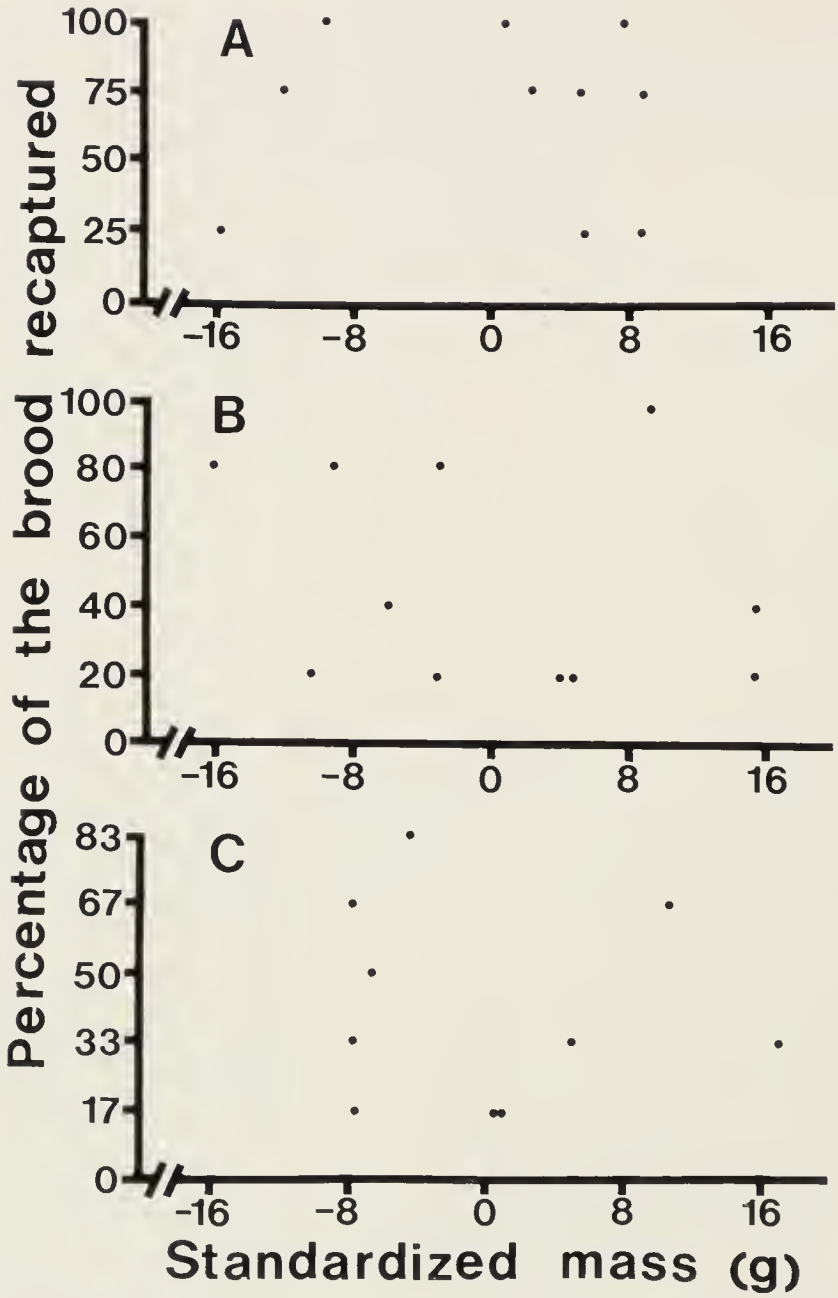

FIG. 1. Relationship between standardized mean egg mass (see text for method of standardization) and percentage of the brood recaptured in broods of 4 (A), 5 (B), and 6 (C) Canada Goose goslings. Spearman rank correlation, A, $r_s = 0.07$; B, $r_s = 0.07$; C, $r_s = 0.06$.

my study, as hatching success was not associated with position in the laying sequence.

In precocial species, hatching usually occurs synchronously (within 12 h), allowing the entire brood to leave the nest simultaneously. Thus, differences in hatching times are small relative to those found in many altricial species. Slight differences in hatching time, however, could be reflected in different levels of awareness in the gosling and also in different

TABLE 4

AVERAGE NUMBER OF GOSLINGS RECAPTURED IN DIFFERENT SIZES OF BROOD, 1983–1984

Brood size[a]	1983			1984			Years combined		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N
1	1.00		1				1.00		1
3				3.00	0.00	2	3.00	0.00	2
4	2.50	1.00	4	2.83	1.47	6	2.70	1.25	10
5	2.57	1.72	7	2.00	1.41	4	2.36	1.57	11
6	2.40	1.14	5	2.60	1.82	5	2.50	1.43	10
7	3.00		1	2.00	1.41	2	2.33	1.15	3
8	3.00		1				3.00		1
P[b]		0.87			0.86			0.90	

[a] Number of goslings leaving the nest.
[b] Determined by a Kruskal-Wallis one-way ANOVA, comparing numbers of goslings recaptured per brood.

degrees of imprinting. Because last laid eggs hatch last (Cargill and Cooke 1981, Syroechkovsky 1975; but see Cooper and Hickin 1972), goslings from these eggs are probably the most likely to suffer mortality. Syroechkovsky (1975) found that late-hatched goslings of Snow Geese experienced higher mortality rates than did other goslings in the brood. In his study, however, the last laid eggs were also the smallest eggs. Position in the laying sequence may not reflect the potential for reaching fledging age in precocial species because there is a strong selection for synchronous hatching. This tends to reduce the advantages given by early positions in the laying sequence. Therefore, it remains to be demonstrated that position *per se* also affects fledging success in precocial species.

Effect of brood size on fledging success.—Although in 1983 larger broods did not produce proportionately the same number of goslings as did smaller broods on the study area, the underlying causes of this phenomenon are not understood. Such lower survival rates for larger broods have also been documented in Common Goldeneye ([*Bucephala clangula*], Andersson and Eriksson 1982) and in experimental larger broods of Semipalmated Sandpipers ([*Calidris pusilla*], Safriel 1975). Rohwer (1985) found no effect of brood size on survival rates of Blue-winged Teal ducklings (*Anas discors*). Other researchers that compared abnormal brood sizes to normal brood sizes did not detect any differences in survival rates between these two groups (Heusmann 1972, Clawson et al. 1979).

Crèching behavior occurred in my study area. Larger broods may not have joined other broods as early as did smaller broods. Consequently, they may not have taken advantage of the dilution effect against predation (Munro and Bédard 1977). Larger broods also may have been easier for

predators to detect (Safriel 1975) and attack. Although these explanations may be valid, I have no data that indicate that predation was an important factor of mortality.

The clutch size of Anserinae appears to be primarily limited by the amount of reserves females can carry to the breeding grounds at high latitudes (Ryder 1970, Ankney and MacInnes 1978, Raveling 1979). However, my results on reduced survival rates with increased brood size imply selective pressure against larger clutches of Canada Geese. The survival rate of broods, along with the amount of body reserves available prior to laying, may have contributed to the evolution of clutch size in Canada Geese in similar environments. Other studies are needed to investigate this factor.

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NEST-SITE SELECTION BY MEW GULLS (*LARUS CANUS*): A COMPARISON OF MARSH AND DRY-LAND COLONIES

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ABSTRACT.—We examined nest-site selection in 13 Mew Gull (*Larus canus*) colonies in south-central Alaska to compare characteristics used in wet versus dry-land colonies. We distinguished three types of colonies that experience different selection pressures: (1) dry-land colonies surrounded by dry land, (2) dry-land colonies surrounded by water, and (3) marsh colonies. The former probably experienced greater mammalian predation than the latter two. Nests in dry-land colonies on the mainland were in dense cover with low nest visibility from 1 and 5 m, except at colonies that were protected by fences or by being on a roof. All colonies were exposed to aerial predators, and in all but one colony cover over nests was significantly greater than for random sites. Dry-land colonies on islands and marsh colonies exposed to flooding had nests that were higher above water than were the random sites. Our results indicate that Mew Gulls' choice of nest sites reflects habitat constraints and predation pressures. *Received 17 Nov. 1986, accepted 26 May 1987.*

Selection of a particular nest site is critical for reproductive success, thus the factors affecting nest-site selection should vary depending on specific environmental features (Lack 1968, Partridge 1978, Cody 1985, Burger 1985). Colonial species often nest in places that are inaccessible to mammalian predators, such as islands or tree tops. Colonies on dry land may also be free from mammalian predators if there are other predator barriers. Despite the emphasis on the differences between marsh, cliff, and dry-land nesting in the literature on colonial birds (Cullen 1957; Burger 1974, 1981; Montevecchi 1978), there are few studies comparing nest-site selection in both marsh and dry-land colonies of the same species (but see Storey 1978, Gotmark 1982). Here we do so for Mew Gulls (*Larus canus*).

Mew Gulls in Alaska use a wide diversity of habitats for colony sites (Burger and Gochfeld, unpubl. data) in a small geographical area. They nest on river bars, tops of spruce trees, in marshes, and on dry land (Grinnell 1900, Murie 1963, Isleib and Kessel 1973, Armstrong 1983). Vermeer and Devito (1986) recently examined several Mew Gull colonies on Vancouver Island and provide additional habitat-use information. Overall, Mew Gulls nest in habitats where they can minimize slope, distance to vegetation, and cover from above; and where they can max-

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imize distance above water and cover around the nest. Thus they provided the opportunity to (1) examine and compare nest-site selection in dry-land and marsh colonies, and (2) compare nest-site selection in dry-land colonies surrounded by other dry land with those surrounded by water. We hypothesized that visibility of the nest would be low and cover around nests would be high in dry-land colonies compared to marsh colonies (and dry-land colonies surrounded by water) that are less vulnerable to mammalian predators. As avian predators have access to all colonies, cover directly over nests should be similar in all habitats.

METHODS AND STUDY COLONIES

We studied 13 colonies of Mew Gulls within 250 km of Anchorage, Alaska, from 26 June to 24 July 1985, during the late incubation and chick phase. We distinguished three types of colonies:

Dry-land colonies surrounded by dry land.—These included (1) the Anchorage military base containing 20 pairs nesting on earthen dikes (or roads), (2) the Anchorage landfill adjacent to the airport with 25 pairs nesting on soil and rock, and (3) the roof top colony with 13 pairs nesting on the Anchorage Port Authority building.

Dry-land colonies surrounded by water.—These included (4) Hood Lake (400 pairs) within Anchorage, a large grassy island surrounded by a lake, (5) Sullivan Park with 24 gull nests on individual grassy islands with small birch trees, (6) a gravel Island in the Nenana River (A) near Denali Park (30 pairs), (7) a rocky island in the Nenana River (B) near Denali Park (75 pairs), (8) a sand bar colony (80 pairs) in the middle of Snow Creek at milepost 18 on the Seward-Anchorage highway, and (9) a man-made rock dike adjacent to the Anchorage Harbor (30 pairs).

Marsh colonies.—These included (10) a wet marsh near the Shell Oil Company plant in the Anchorage Port area (3 floating nests), (11) a creek bog near Anchorage Airport with 12 nests built on the top of marsh grass tussocks, (12) two nests in a moss muskeg bog near the Anchorage Post Office, and (13) a salt-marsh colony (30 nests) at Portage marsh, at milepost 40 south of Anchorage.

At each colony we collected data on all nests (if under 30) or a random sample of 30 nests including slope (in degrees from the horizontal); distance to nearest rock, tree or vegetation; distance to edge of colony; height above water; height of nearest tree, rock or vegetation; percent cover directly over the nest; percent cover in a 1- and 5-m radius around the nest; and visibility of the nest from above the nest and from 1 and 5 m. We distinguished ground cover (herbs less than 5 cm tall), herb cover (taller than ground cover, but shorter than trees), and tree cover.

At each colony we selected a number of random sites equal to the number of nests sampled, or 15 sites (if there were fewer nests) with which to compare to nests characteristics. Random sites were chosen by selecting X and Y coordinates for each site from a table of random numbers (Burger and Gochfeld 1986). Similar characteristics were measured at the random sites and the nests. We compared nest-site characteristics with those of random sites with Kruskal-Wallis χ^2 tests.

RESULTS

Dry-land Colonies Surrounded by Dry Land

Dirt dike on military base.—Port Anchorage has a military installation enclosed by chainlink fences, immediately inside of which is an earthen

dike about 2 m high × 2.5 m wide, beside a ditch or moat. The dikes were devoid of vegetation except for a few small willows or tall herbs that grew on the shoulder. Mew Gulls nested on these dikes, close to the vegetation, on the top or gently sloping sides, where they built up one side of the nest so the nest was level. They nested in sites with low vegetation cover (high visibility), but within 0.5 m of vegetation (Table 1). Their choice of nest sites differed significantly from the random sites with respect to slope, percent rock cover, vegetation cover (but not vegetation height), and visibility above the nest.

Airport landfill.—Adjacent to the Anchorage airport a landfill (coarse spoil sand) with scattered low herbs contained 25 pairs of Mew Gulls and about 40 pairs of Arctic Terns (*Sterna paradisea*). One edge of the colony was bordered by willow and birch trees and a creek, and the other was bordered by a jogging trail and a six-lane highway. Overall, vegetation cover in 5-m^2 plots on the site ranged from none to 40%. Mew Gulls nested on flat areas away from rocks (Table 1). Cover over nests was greater than in the 5-m^2 areas around nests, indicating that gulls choose to nest close to vegetation (small herbs and *Lupinus*), although the area around the nest was open and visibility of the nest was high. The nest sites differed significantly from random sites in having more cover, being closer to vegetation, with greater visibility, and with taller herbs and vegetation.

Anchorage port roof.—Less than 100 m from the rock dike was a large harbor warehouse with a flat, fine-gravel roof. The roof was crisscrossed with electrical conduits with 4-cm high junction boxes situated at intervals. Only one side of the warehouse was exposed to boats and cranes, which operated only 5 m from this edge. Because the birds were entirely exposed on the roof, we were worried about young running over the edge, and we mapped the location of the cables and junction boxes for later generation of random site data (Monte Carlo simulation, Ricklefs and Lau 1980). We took data at nest sites and left immediately. While we were there, the young formed a group on the farthest side of the roof. Nests were significantly closer than expected to the edge of the roof farthest from the harbor activity. All nests were placed adjacent to conduit cables, and many were adjacent to the junction boxes (Table 2). Many gulls also nested next to vertical objects (but not next to tall chimneys).

Dry-land Colonies Surrounded by Water

Hood Lake.—Most of the periphery of the grassy island was covered with short grass. Scattered around the edge of the island were short willow trees, and at one end there was a small stand (5 × 20 m) of willow and birch trees. Gulls nested over the entire island, except in the tall grass on the central ridge. Mew Gulls generally nested on flat sites in grass that

TABLE 1

CHARACTERISTICS OF NESTS AND RANDOM SITES ($\bar{x} \pm$ SD) FOR MEW GULLS NESTING ON DRY-LAND COLONIES

Characteristics	Hood Lake			Airport landfill		
	Nests	Random sites	χ^2 (*P*)	Nests	Random sites	χ^2 (*P*)
Height above water (cm)						
Distance to water or edge (cm)					685 ± 32	
Slope (°)	2 ± 0.5	4 ± 0.5	3.75 (0.05)	4 ± 0.8	6 ± 3	3.3 (NS)
% rock cover	0	0	—	0.4 ± 0.2	1 ± 0.3	4.03 (0.05)
Rock height (cm)	—	—	—	—	2 ± 0.3	
% cover over nest	98 ± 0.1	94 ± 1	9.65 (0.001)	91 ± 3	45 ± 6	14.71 (0.0001)
% cover within 1 m	98 ± 0.2	94 ± 1	5.74 (0.02)	84 ± 4	48 ± 6	11.20 (0.0008)
% cover within 5 m	99 ± 0.1	95 ± 1	4.82 (0.03)	77 ± 4	48 ± 5	8.60 (0.003)
Distance to vegetation (m)	0.5 ± 0.2	4.0 ± 0.7	25.1 (0.0001)	0.5 ± 0.4	6 ± 3	6.7 (0.01)
Distance to willows (m)	4.4 ± 1.1	4.1 ± 8.2	1.2 (NS)			
Distance to birch (m)	1.1 ± 0.2	1.5 ± 3.8	0.8 (NS)			
Distance to *Lupinus* (cm)	37 ± 0.5	49 ± 6.5	1.4 (NS)	48 ± 14[a]	154 ± 34	5.94 (0.01)
Nest visibility from over nest	94 ± 3	99 ± 2	10.5 (0.001)	90 ± 2	94 ± 2	5.14 (0.02)
Nest visibility from 1 m	94 ± 3	98 ± 4	7.70 (0.005)	88 ± 4	97 ± 0.7	13.23 (0.0003)
Nest visibility from 5 m	95 ± 2	99 ± 2	7.91 (0.004)	85 ± 4	97 ± 1	11.08 (0.0009)
Vegetation height (cm)	57 ± 3	38 ± 4	14.3 (0.0002)	68 ± 7	43 ± 5	6.74 (0.009)
Herb height (cm)	12.8 ± 1	9.4 ± 1	8.38 (0.003)	32 ± 6	9 ± 1	15.01 (0.0001)
Nearest neighbor nest (cm)	283 ± 29			1147 ± 201		

[a] Distance to grass.
[b] For the 10 nests close to birch.

TABLE 1
CONTINUED

Characteristics	Military base dirt dike			Sullivan Park		
	Nests	Random sites	χ^2 (*P*)	Nests	Random sites	χ^2 (*P*)
Height above water (cm)				38 ± 5		
Distance to water or edge (cm)	110 ± 19	90 ± 10	1.2 (NS)	101 ± 24		
Slope (°)						
% rock cover	25 ± 2	32 ± 3	5.62 (0.03)	0.7 ± 0.3		
Rock height (cm)	14 ± 6	3 ± 2	83 (0.001)	0		
% cover over nest						
% cover within 1 m	5 ± 3	0.1 ± 0.2	2.1 (NS)	94 ± 3	80 ± 10	12.3 (0.0001)
% cover within 5 m	15 ± 7	0.3 ± 0.2	12.2 (0.001)	87 ± 6		
Distance to vegetation (m)	6 ± 3	0.2 ± 0.1	9.3 (0.003)	64 ± 5		
Distance to willows (m)	3 ± 0.1	5.2 ± 1.6	11.2 (0.001)	1.2 ± 0.5		
Distance to birch (m)						
Distance to *Lupinus* (cm)						
Nest visibility from over nest	96 ± 3	99 ± 0.1	11.6 (0.001)	72 ± 8	86 ± 7	16.1 (0.0001)
Nest visibility from 1 m	99 ± 0	99 ± 3	0.0 (NS)	71 ± 8		
Nest visibility from 5 m	99 ± 0	99 ± 2	0.0 (NS)	63 ± 11		
Vegetation height (cm)	55 ± 7	51 ± 6	0.6 (NS)	73 ± 5	56 ± 6	7.21 (0.005)
Herb height (cm)	65 ± 63 ± 6	63 ± 6	0.2 (NS)	21 ± 11		
Nearest neighbor nest (cm)	1280 ± 60			374 ± 72		

TABLE 2

CHARACTERISTICS FOR NESTS AND RANDOM SITES ($\bar{x} \pm$ SD) FOR MEW GULLS NESTING ON A ROOF AND ON A ROCK DIKE

Characteristic	Roof			Rock dike		
	Nests	Random sites	P[a]	Nests	Random sites	χ^2 (P)
Distance to edge (cm)	222 ± 401	1038 ± 190	0.005			
Distance to water (cm)				610 ± 19	547 ± 15	3.43 (0.06)
Height above water (cm)	—	—		23 ± 18	27 ± 12	1.2 (NS)
Slope (°)	0	0	NS	3 ± 5	7 ± 0.6	4.57 (0.03)
% cover over nest	0	0	NS	5 ± 1	16 ± 6	5.71 (0.02)
% cover within 1 m	0	0	NS	65 ± 2		
% cover within 5 m	0	0	NS	4 ± 2		
% rock				11 ± 5		
Herb height (cm)				41 ± 5		
Vegetation height (cm)				46 ± 7		
Distance to bush or trees (cm)				127 ± 25		
Distance to vegetation (cm)				244 ± 87		
Nest visibility from over nest	99 ± 0	99 ± 0	NS	96 ± 2		
Nest visibility from 1 m	99 ± 0	99 ± 0	NS	98 ± 1		
Nest visibility from 5 m	99 ± 0	99 ± 0	NS	99 ± 0		
Distance to junction box (cm)	309 ± 15	462 ± 16	0.0005			
Distance to vertical rock (cm)	3.8 ± 1.8			13 ± 4	14 ± 3	0.2 (NS)
Height of vertical object (cm)	42 ± 38			31 ± 5	30 ± 3	0.3 (NS)
Distance to cliff edge (cm)				36 ± 5	47 ± 5	3.80 (0.06)
Height of cliff drop (cm)				13 ± 2	19 ± 2	5.42 (0.04)

[a] From Monte Carlo simulation.

averaged 57 cm tall, and that had scattered low herbs (12 cm high) around them (Table 1). Grass cover around the nest was 98%, but the grass did not cover the nest, and visibility estimates averaged about 95%. Nest sites differed significantly from the random sites in being flatter, with more cover, lower visibility, and taller vegetation, but not with respect to the distance to trees or bushes (Table 1).

Sullivan Park.—Located within Anchorage, Westchester Lagoon in Sullivan Park has 31 small grassy islands (2–4 m × 3–12 m), and is used extensively for canoeing. Due to the large number of people on the lake, we landed on nesting islands only to take nest measurements, and we recorded only limited data from random sites. Most of the smaller islands had only one pair of nesting gulls; however, five of the larger islands had two (one nest at each end of the island). Mew Gulls nested on flat sites well above water, but usually at the edge of islands (Table 1). Cover over the nest was denser than in the 5-m area around the nest. Gulls did not nest close to birch trees, but they nested close to other vegetation and herbs. They selected to nest on sites with more cover, lower visibility, and near taller vegetation than occurred at the random sites (Table 1).

Nenana River site A.—The first Nenana River colony we examined was just outside Denali Park, on a low, tear-shaped island with black sand, gravel, and small rocks. The river was wide and swift-moving at this point. In the center, dead logs deposited by high water formed shelters for some chicks. Small plants (*Lupinus*) and herbs grew on the edges of the island. Thirty pairs of gulls nested on the island, although they concentrated on the downriver end where the land was slightly higher in elevation. A 0.5-m rise in river elevation would have flooded all of the nests. Mew Gulls nested on the higher parts of the island, on slight slopes on sites with little cover, close to herbs and willow bushes (Table 3). Their choices of nest sites differed from the random points with respect to distance to water (they nested farther away), slope (flatter spots), rock cover (more rocks), and vegetation height (they chose taller vegetation) (Table 3).

Nenana River site B.—Nenana B colony, located about 5 km downriver from Nenana A where the river widens, was much larger and was covered (90%) with dense trees and shrubs, which were avoided by nesting gulls. The leading edge of the island exposed to the swift currents was a 5–60 m wide section with boulders and small rocks where most gulls nested. On these beaches sand was deposited on a few higher places which supported small willows, but otherwise there was little vegetation cover. The average gull nest was 28 cm above the water, over 30 m from the water's edge, and on flat sites with intermediate cover (Table 3). Cover over nests was greater than in the 1 and 5 m areas around the nest, indicating selection

TABLE 3

CHARACTERISTICS AT NESTS AND RANDOM SITES FOR DRY-LAND MEW GULL COLONIES SURROUNDED BY WATER IN ALASKA

	Snow Creek			Nenana River A			Nenana River B		
Characteristics	Nests	Random sites	χ^2 (*P*)	Nests	Random sites	χ^2 (*P*)	Nests	Random sites	χ^2 (*P*)
Height above water (cm)	18 ± 3	13 ± 1.5	2.8 (NS)	24 ± 3			28 ± 4	18 ± 3	21.2 (0.001)
Distance to water (m)	15.1 ± 2.3	15.9 ± 2.3	0.2 (NS)	7.2 ± 2.1	2.8 ± 3.7	28.9 (0.0001)	34 ± 6	28 ± 2	29.6 (0.0001)
Distance to edge (m)	14.8 ± 2.4	19.5 ± 2.5	1.2 (NS)	28.2 ± 7					
Slope (°)	0.5 ± 0.2	1.6 ± 0.5	4.5 (0.03)	5 ± 2	8 ± 1	4.7 (0.03)	10 ± 7	20 ± 6	5.82 (0.02)
% rock cover	0	0		24 ± 3	1 ± 1	31.2 (0.0001)			
Rock height	—	—	—	3 ± 0.6	2 ± 0.8	0.8 (NS)			
% cover over nest	45 ± 4	11 ± 4	19.8 (0.0001)	3 ± 1	16 ± 5	7.41 (0.006)	46 ± 6	16 ± 5	9.84 (0.001)
% cover within 1 m	37 ± 4	11 ± 3	18.1 (0.001)	15 ± 4	15 ± 5	0.0 (NS)	39 ± 6	15 ± 5	10.07 (0.001)
% cover within 5 m	24 ± 2	12 ± 2	10.9 (0.001)	18 ± 5	12 ± 3	1.1 (NS)	26 ± 5	13 ± 5	4.43 (0.03)
Distance to vegetation (m)	10 ± 3	47 ± 15	5.0 (0.05)	28 ± 6	44 ± 12	5.7 (0.03)	5 ± 3	44 ± 12	8.05 (0.004)
Distance to willows (m)	0.7 ± 0.3	1.1 ± 5.9	2.1 (NS)	1.2 ± 2.5	35.6 ± 6.7	21.6 (0.0001)	1.4 ± 3.6	3.6 ± 6.7	6.0 (0.01)
Willow height (m)	1.2 ± 0.7	0.8 ± 1.3	6.1 (0.01)	0.8 ± 0.1	0.56 ± 3.1	0.8 (NS)	0.7 ± 0.1	0.5 ± 0.7	0.2 (NS)
Distance to *Lupinus* (cm)	2.9 ± 0.6	2.8 ± 6.7	0.1 (NS)						
Nest visibility from over nest	80 ± 6	88 ± 5	4.3 (0.03)						
Nest visibility from 1 m	90 ± 1	93 ± 4	0.6 (NS)						
Nest visibility from 5 m	92 ± 3	95 ± 3	0.4 (NS)						
Vegetation height (cm)	45 ± 5	41 ± 9	0.5 (NS)	78 ± 13	47 ± 7	12.1 (0.001)			
Herb height (cm)	15 ± 3	3 ± 0.5	13.8 (0.0002)						
% bushes	24 ± 4	7 ± 3	5.8 (0.01)						
Nearest neighbor nest (cm)	1097 ± 140			992 ± 136			817 ± 120		

of herbs or shrubs. Gull nests were on higher sites, farther from water, on flatter slopes in greater cover, and closer to vegetation than were the random sites (Table 3). Nests tended to be clustered in favorable areas, where two pairs nested near the same vegetation or driftwood clump.

Snow Creek.—At milepost 18 (about 100 km south of Anchorage toward Seward), the highway crosses Snow Creek and a low lying, partly vegetated sand bar (over 500 m long) that has a high, central portion, which supports a dense stand of willow and birch trees. The gulls nested on the upstream portion of the island on black sand among scattered short willows (<2 m tall). The nesting substrate was only 18 cm above the river level. Gulls nested close to vegetation with intermediate cover and high visibility (Table 3). They nested closer to willow than to *Lupinus,* and they selected flatter sites with more cover (and less visibility), that were next to taller willow and herbs when compared to the random sites (Table 3).

Rock dike.—The rock dike at the Anchorage harbor is a boulder embankment about 100 m × 10 m, which shores a heavily used road and parking lot. The rocks were placed at a 30° slope, and at the bottom was a tidal mudflat. On the top margin some willow trees grew between the dike and the parking lot. About 30 pairs of gulls nested among the rocks, and they were vigorously protected by the port personnel that had adopted the colony. Gulls were limited to a narrow range of sites because if they nested close to the bottom they were exposed to tidal flooding, whereas nesting close to the top exposed them to people from the parking lot. Gulls nested on flat rocks, usually well above the high water (Table 2). There was almost no cover over the nests (except rock overhangs), and visibility of the nests was high. Nests were placed on flat rocks, with small "cliffs" below the nest and upright rock faces above. There were no differences in the height of the rocks above nests, but the cliffs below the nests were shorter than for the random sites (Table 2). Nests were farther from water than were random sites.

Marsh Colonies

Anchorage port marsh.—A small pond on Shell Oil property at the Port of Anchorage had 3 pairs of nesting gulls. The water in the marsh was deeper than 1.5 m, and had cattails and emergent vegetation in the center. The pond was fringed with oil storage tanks and upland areas supporting 10-m tall trees. The gulls built floating platforms that were 35–50 cm wide and extended 30–60 cm below the water surface. The dead, emergent vegetation around the nest extended only 16.0 ± 4.4 cm [SD] above the water surface, suggesting extensive flooding since the previous growing season. Cover over the nests ranged from 2 to 5%, and visibility ranged

TABLE 4

CHARACTERISTICS OF NESTS AND RANDOM SITES ($\bar{x} \pm$ SD) FOR MEW GULLS NESTING IN MARSHES

	Portage marsh			Moss muskeg			Creek bog		
Characteristics	Nests	Random sites	χ^2 (*P*)	Nests	Random sites	χ^2 (*P*)	Nests	Random sites	χ^2 (*P*)
Distance to grass or trees (m)	0.12 ± 0.03[a]			1.45 ± 0[b]	3.0 ± 9	1.5 (NS)	3.1 ± 1.1[b]	2.0 ± 0.6	0.9 (NS)
Tree height (m)				122 ± 18	67 ± 3	48 (0.03)			
Height above water (cm)	2.0 ± 1	0.1 ± 0.4	4.6 (0.01)	38 ± 12	−12 ± 2	4.82 (0.02)	27 ± 4	12 ± 10	7.57 (0.005)
Slope	0.1 ± 0.1	0.1 ± 0.1	0.0 (NS)	0	0		0.4 ± 0.4	3 ± 0.6	6.08 (0.01)
% cover over nest	95 ± 2	89 ± 1.3	5.6 (0.01)	97 ± 2	65 ± 7	4.48 (0.03)	98 ± 1	91 ± 6	1.6 (NS)
% cover within 1 m	96 ± 3	75 ± 4	5.30 (0.02)	90 ± 0	78 ± 2	1.4 (NS)	83 ± 7	95 ± 2	1.9 (NS)
% cover within 5 m	95 ± 2	80 ± 8	9.97 (0.001)	85 ± 5	81 ± 2	0.9 (NS)	68 ± 6	94 ± 2	5.80 (0.01)
% bushes				27 ± 3	15 ± 7	3.38 (0.06)	22 ± 10	17 ± 6	1.2 (NS)
Herb height (cm)							21 ± 4	20 ± 2	0.1 (NS)
Vegetation height (cm)	38 ± 5	43 ± 1	0.3 (NS)	35 ± 1	24 ± 3	3.36 (0.05)	50 ± 6	38 ± 4	2.1 (NS)
Nest visibility from over nest	97 ± 1	98 ± 3	0.1 (NS)	80 ± 4	92 ± 6	6.48 (0.01)	86.7	80 ± 6	1.2 (NS)
Nest visibility from 1 m	91 ± 1	87 ± 3	1.4 (NS)	94 ± 4	92 ± 6	0.1 (NS)	87 ± 7	77 ± 6	2.2 (NS)
Nest visibility from 5 m	70 ± 4	82 ± 4	1.2 (NS)	90 ± 0	92 ± 7	0.1 (NS)	87 ± 7	72 ± 8	2.4 (NS)
Distance to vegetation (cm)	0	0		0 ± 0	0.6 ± 0.4	0.6 (NS)	2 ± 1	15 ± 6	3.28 (0.07)
Nearest neighbor distance (cm)	1450 ± 1525			350 ± 350			858 ± 108		

[a] Grass.
[b] Alder trees.

from 90 to 99% ($\bar{x}$ = 96 ± 3%). In this habitat gulls nested where they could attach their nests to the emergent vegetation, and avoided open water. This restricted them to an 8 × 10 m section in the middle of the pond.

Anchorage creek bog.—The creek-bog colony (27 m × 85 m) was between the airport and a slow moving creek within 100 m of the airport landfill colony. The site was grass and sphagnum moss adjacent to the creek with dense birch, willow, and alder trees on the other side. The gulls nested on top of the grass hummocks about 1 m above water, on flat spots with higher cover around the nest and high visibility overhead (Table 4). Nest sites differed from random sites with respect to height above water, slope, cover within 5 m, and distance to vegetation. Nests were significantly farther from birch trees (5.7 ± 1.2 m) than were random points (2.9 ± 6.9 m, $\chi^2 = 4.37$, $P < 0.03$), and were closer to water (4.4 ± 1.8 m) than were random points (9.3 ± 2.6 m, $\chi^2 = 4.59$, $P < 0.03$). These two characteristics placed them farther from the dry land, and may have discouraged access by the dogs we saw walking among the birch trees.

Moss muskeg.—Two pairs of gulls nested in the muskeg colony across from the Anchorage Post Office. The extensive marsh was primarily sphagnum moss with occasional hummocks where spruce trees and dead bushes provided higher places for nests. While walking in the marsh we sank kneedeep in water. The nests, 350 cm apart, were well above the water on hummocks near tall trees with dense cover and high visibility (Table 4). The nest sites differed from the 15 random sites with respect to tree height, height above water, cover over nests, percent bushes, and visibility from the nest (Table 4).

Portage marsh.—The Portage marsh, located along the road to Seward, 64 km south of Anchorage, is an extensive grassy marsh where about 30 pairs of gulls nested on the ground amid the grass. The gull colony was adjacent to an Arctic Tern colony of about 25 pairs. Gulls nested around a small pond, placing their nests on extensive platforms of dead grass, presumably constructed to raise them above flood levels. The gull nests were on the highest available part of the marsh (Table 4). Nest sites were on flat ground in dense cover but with high visibility overhead. Nest sites differed from random sites with respect to cover.

DISCUSSION

Nest-site Selection

Mew Gull nest sites differed from random sites with respect to several physical and biotic factors at all colony sites. The same features, however,

were not necessarily important in each colony (Table 5). Comparisons of the characteristics recorded at colonies indicate that for some colonies many environmental features were important, whereas at other sites (roof top, marsh colonies) few characteristics differed (see below).

Colonies ranged from dense vegetation (Hood Lake, Sullivan Lake, creek bog, moss muskeg, Portage marsh), to sparse vegetation (military base, landfill, Nenana River A and B, Snow Creek), to being nearly (rock dike) or completely devoid of vegetation (roof). All colonies, however, had some cover. Although in most colonies cover was provided by vegetation, cover was also provided by rocks (rock dike) and junction boxes (roof). Vegetation and rocks clearly provided protection from both predators and inclement weather, as chicks could hide almost completely from view. The junction boxes, however, provided only shade and protection from the wind.

Marsh Versus Dry-land Colonies

Predators.—In this study we divided the colonies into three types: dry-land colonies surrounded by land, dry-land colonies surrounded by water, and marsh colonies. One method of protecting nests from mammalian predators is to have nest sites invisible from the ground (low visibility from 1 and 5 m). Only the landfill colony, however, where we saw both dog and cat tracks, had lower visibilities from 1 and 5 m than did random sites. Gulls nesting on the military base and roof did not have low visibility of their nests, but they were protected from some mammalian predators by chain-link fences (military base) or by being 9 m above ground (roof). Mammalian predators could not approach either colony.

As all colonies (regardless of habitat) were exposed to aerial predators, we expected cover over nests to be greater than for the random points, and this was the case except at the creek-bog colony. At this colony nesting on the tops of hummocks (away from flooding) appeared to override selection for vegetative cover (see below).

Inclement weather.—Inclement weather can provide stress for eggs and chicks during hot or cold spells, or during heavy rains (Austin 1933, Burger 1974, Burger and Lesser 1978). This stress should be similar regardless of habitat type. Weather stresses can be reduced by having hiding places for chicks, or by providing cover over the nests. In all colonies the gulls nested in cover whenever it was available.

Floods.—The marsh colonies and dry-land colonies surrounded by water were subject to flood conditions. Two of the colonies examined (Hood Lake, Sullivan Park) were on high and dry islands that would rarely, if ever, flood. The other colonies, however, probably experienced regular flooding. The riverine colonies were particularly vulnerable to flooding

TABLE 5

COMPARATIVE NEST CHARACTERISTICS OF MEW GULL COLONIES THAT DIFFERED FROM RANDOM (X), DID NOT DIFFER (NS), OR WERE NOT MEASURED (—[a])

	Dry land			Dry land surrounded by water								
	Anchorage military base	Anchorage landfill	Roof top	Hood Lake	Sullivan Park	Nenana River A	Nenana River B	Snow Creek	Rock dike	Creek-bog	Moss muskeg	Portage marsh
Slope	X	NS	—	X	—	X	X	X	X	X	—	NS
% rock cover	X	X	—	—	—	X	—	—	—	—	—	—
Rock height	—	—	—	—	—	—	—	—	—	—	—	—
% cover over nest	X	X	—	X	X	X	X	X	X	NS	X	X
% cover within 1 m	X	X	—	X	—	NS	X	X	—	NS	NS	X
% cover within 5 m	X	X	—	X	—	NS	X	X	—	X	NS	X
Distance to vegetation	X	X	—	X	—	X	X	NS	—	NS	X	—
Distance to willow	—	—	—	NS	—	X	X	NS	—	—	—	—
Distance to birch	—	—	—	NS	—	—	—	—	—	—	—	—
Distance to *Lupinus*	—	X	—	NS	—	—	—	NS	—	—	—	—
Willow height	—	—	—	—	—	NS	NS	X	—	—	—	—
Vegetation height	—	X	—	X	—	X	—	NS	—	NS	X	NS
Herb height	X	X	—	X	X	—	—	X	—	NS	—	—
Nest visibility over nest	X	X	NS	X	—	—	—	X	—	NS	X	NS
Nest visibility from 1 m	NS	X	NS	X	—	—	—	NS	—	NS	NS	NS
Nest visibility from 5 m	NS	X	NS	X	—	—	—	NS	—	NS	NS	NS
% bushes	NS	—	—	—	—	—	—	X	—	NS	X	—
Distance to water	—	—	—	—	—	X	X	NS	X	—	—	—
Height above water	—	—	—	—	—	—	X	NS	NS	X	X	X
Distance to junction box	—	—	NS	—	—	—	—	—	—	—	—	—

[a] Usually because they were not relevant. Data summarized from Tables 1–4.

because they were located on low sand or gravel islands that were completely washed over by flood waters. In all three riverine colonies, the gulls nested on the highest available sites that provided some vegetative cover. We also observed (unpubl. data) that gulls nesting on these colonies moved chicks to higher ground after hatching.

Some marsh colonies were vulnerable to flooding because nests were on vegetation just above the water level (Shell Oil marsh, moss muskeg, creek bog). Indeed, the nests at the moss muskeg colony had recently been flooded out, and the gulls were in the process of relaying eggs. In all marsh colonies nests were significantly higher above water than were random sites.

Our results indicate that protective cover at nests is critical for Mew Gulls, and that cover can be provided by vegetation, rocks, or man-made structures. Nest visibility from 1 or 5 m, which would act to reduce nest detection by ground predators, was more important for dry-land than for marsh colonies. For marsh colonies, height above water was more important in affecting nest-site selection. Overall, gulls used different physical features in the different colonies to provide protection from predators, inclement weather, and floods.

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SHORT COMMUNICATIONS

Wilson Bull., 99(4), 1987, pp. 688–690

Distribution of *Microligea palustris* in Haiti.—*Microligea palustris,* the Green-tailed Ground Warbler, which is endemic to Hispaniola, has been previously reported in Haiti only from the Massif de la Selle (Wetmore and Swales 1931; Bond 1980, 1984; AOU 1983) (Fig. 1). In this mountain range, it is found in dense shrub or disturbed patches of montane wet forest above 1700 m (Wetmore and Swales 1931, pers. obs). There have been no confirmed reports of *Microligea palustris* in the Massif de la Hotte in the west, or in other parts of Haiti, where similar habitat exists (Bond 1984). In the Dominican Republic, it is a habitat generalist, and it is found as low as sea level and in semiarid areas (Wetmore and Swales 1931, Bond 1980, Dod 1981).

On 14 August 1985, southeast of Bombardopolis (97 km northwest of Gonaives) on Morne Chien, at an elevation of 115 m, I observed 4–5 *M. palustris* and collected a single specimen. The specimen was deposited in the skeletal collection in the Carnegie Museum of Natural History (CMNH No. S-11063). The species was common in transitional scrub between desert thornscrub and the more mesic woodland around Bombardopolis. I observed 3–4 more *M. palustris* the following day at an elevation of 330 m, on the road from Bombardopolis to Mole St. Nicholas, in similar habitat. They were traveling in mixed species flocks with Black-crowned Palm-Tanagers (*Phaenicophilus palmarum*).

James Bond (1986) believes that the skeletal specimen may be a race related to *M. p. vasta* found in xeric habitats in the Dominican Republic. (He did not examine the specimen.) Although the skin is not available for confirmation of its racial affinities based on plumage criteria, a preliminary genotypic comparison of this individual to three specimens from southern Haiti suggests that the northern specimen shares alleles with its southern counterparts in 13 of 14 loci examined to date.

A taxonomic comparison of *Microligea* to other tanagers and warblers demonstrates that it clusters behaviorally and genetically with tanagers, and not with wood warblers (unpubl. data). Furthermore, as a tanager, its genetic variability is quite low ($\bar{H}$ (observed) = 0.017 vs 0.109 for tanagers; McDonald, unpubl. data), suggesting that *Microligea* may have gone through a population bottleneck and has not yet recovered (Nei et al. 1975). An alternative explanation is that *Microligea* has recently invaded the northwest peninsula and is suffering low genetic variability due to the founder effect.

The occurrence of *M. palustris* in xeric and transitional habitats in the northwest peninsula of Haiti is interesting because of its ecological and biogeographical implications. Extensive collecting efforts by W. L. Abbott in the early part of the century (January–June, 1917) failed to turn up *Microligea* in this region (Wetmore and Swales 1931). If *Microligea* were a recent arrival in this region, it is unlikely it has emigrated from the mountains in southern Haiti. Morne Chien is an island of transitional scrub and mesic woodland in the middle of the northwest peninsular desert. *M. palustris* found in this area is not confined to mesic woodland, but is abundant in dry transitional scrub below the woodland, suggesting that (1) arid habitats may not form a barrier to dispersal of these forms and (2) that this form is adapted to xeric conditions. Therefore, if *Microligea* is a recent arrival, it most likely came from the lowland arid zones of the Dominican Republic to the east.

A more extensive genetic and morphological analysis of the northern group of specimens from the Dominican Republic and southern Haiti is needed: (1) to determine if *M. p. vasta* differs genetically from the Haitian specimens and (2) to determine if there are significant gene frequency differences between the northern and southern Haiti populations.

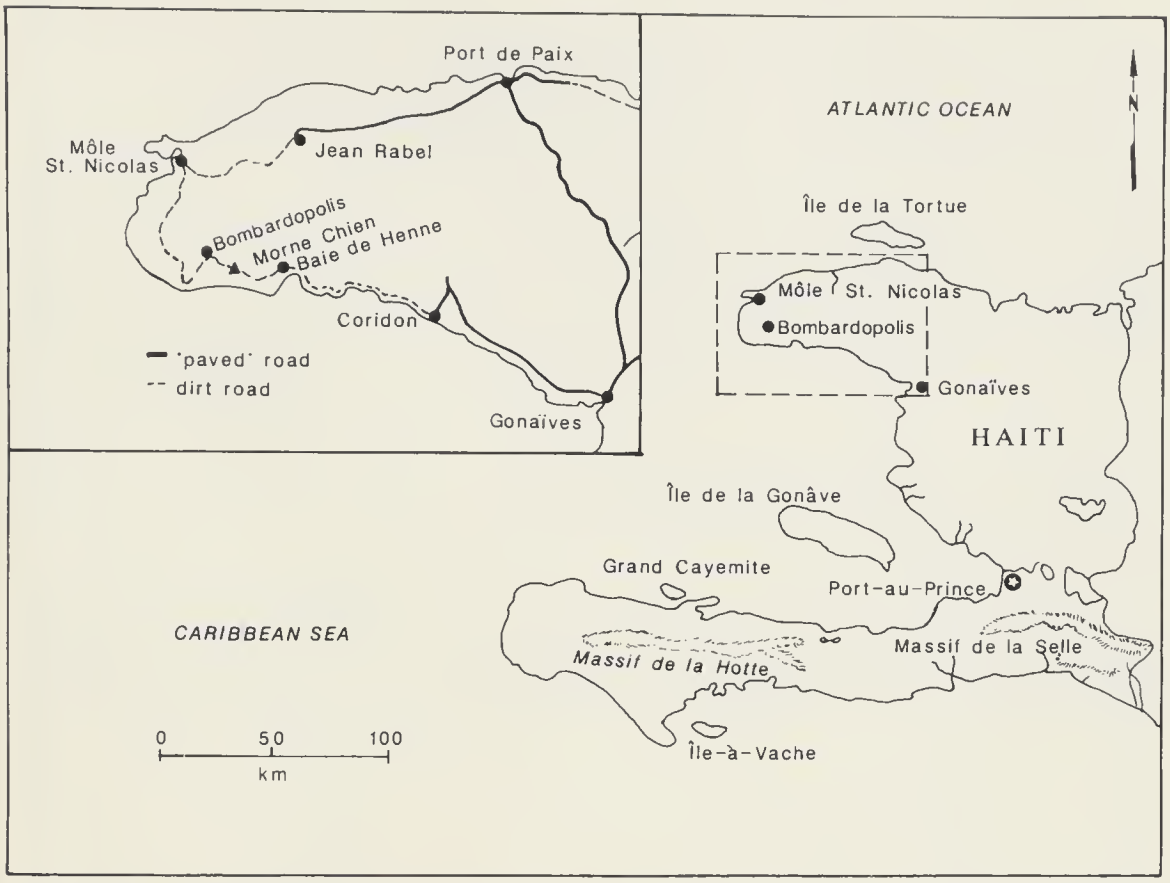

FIG. 1. Map of Hispaniola designating major landmarks in Haiti regarding distribution of *Microligea palustris.*

M. palustris is common where it is found (Dod 1981, unpubl. data); however, most montane habitats in Haiti are in danger of vanishing, and the species is protected in Haiti (Magny 1985). The "protected" status in Haiti is equivalent to the "vulnerable" status listed by IUCN/ICBP (King 1981), requiring special permits for collecting. Its presence in a xeric region of Haiti, with a low human population density, makes it potentially less vulnerable to extirpation there. Until more is known about the range of this species in Haiti, it should remain protected.

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Expansion of the zone of hybridization of Northern Flickers in Alberta.—Hybridization between the eastern yellow-shafted form of the Northern Flicker (*Colaptes auratus auratus*) and the western red-shafted form (*C. a. cafer*) has been well documented for the Great Plains of the United States (Short 1965, Anderson 1971, Moore and Buchanan 1985). In the Great Plains, the zone of hybridization has remained essentially stable over the past 100 years (Moore and Buchanan 1985); however, contact between yellow- and red-shafted birds farther north has been little studied (Rising 1983). Short (1965) examined only 45 specimens in his analysis of the distribution of parental and hybrid forms of flickers in Saskatchewan and Alberta, Canada. Here we report on the examination of 98 Northern Flicker skins collected during the breeding season (1 May to 31 July) between 1891 and 1984 in Alberta. A maximum of 10 of these skins were included in the Short (1965) analysis; therefore at least 88 provide additional data on the delineation and temporal stability of the hybrid zone in Alberta.

Specimens were divided into two groups: (1) those collected prior to 1960 (1891–1957) and (2) those collected after 1960 (1961–1984). These groups facilitate comparison with Short's (1965) work and allow us to examine changes in the hybrid zone over time. Following Short (1965), we scored 6 plumage color characters for each specimen on a scale of 0 (pure *auratus*-like) to 4 (pure *cafer*-like). The characters examined, with parental states given in parentheses in the order *auratus-cafer* were crown color (gray-brown), ear covert color (tan-gray), throat color (tan-gray), nuchal patch (present-absent), shaft color (yellow-salmon) and malar color (males only, black-red). Scores of 1–3 represent proportionally intermediate states. Scores were summed across the 6 plumage characters to yield a hybrid index score. All scores from female specimens were converted to a scale of 24 to make them comparable to those of males. These scores range from 0 (*auratus*-like) to 24 (*cafer*-like). Specimens were grouped according to collection sites, and scores were then plotted on a map of Alberta (Figs. 1A and 1B).

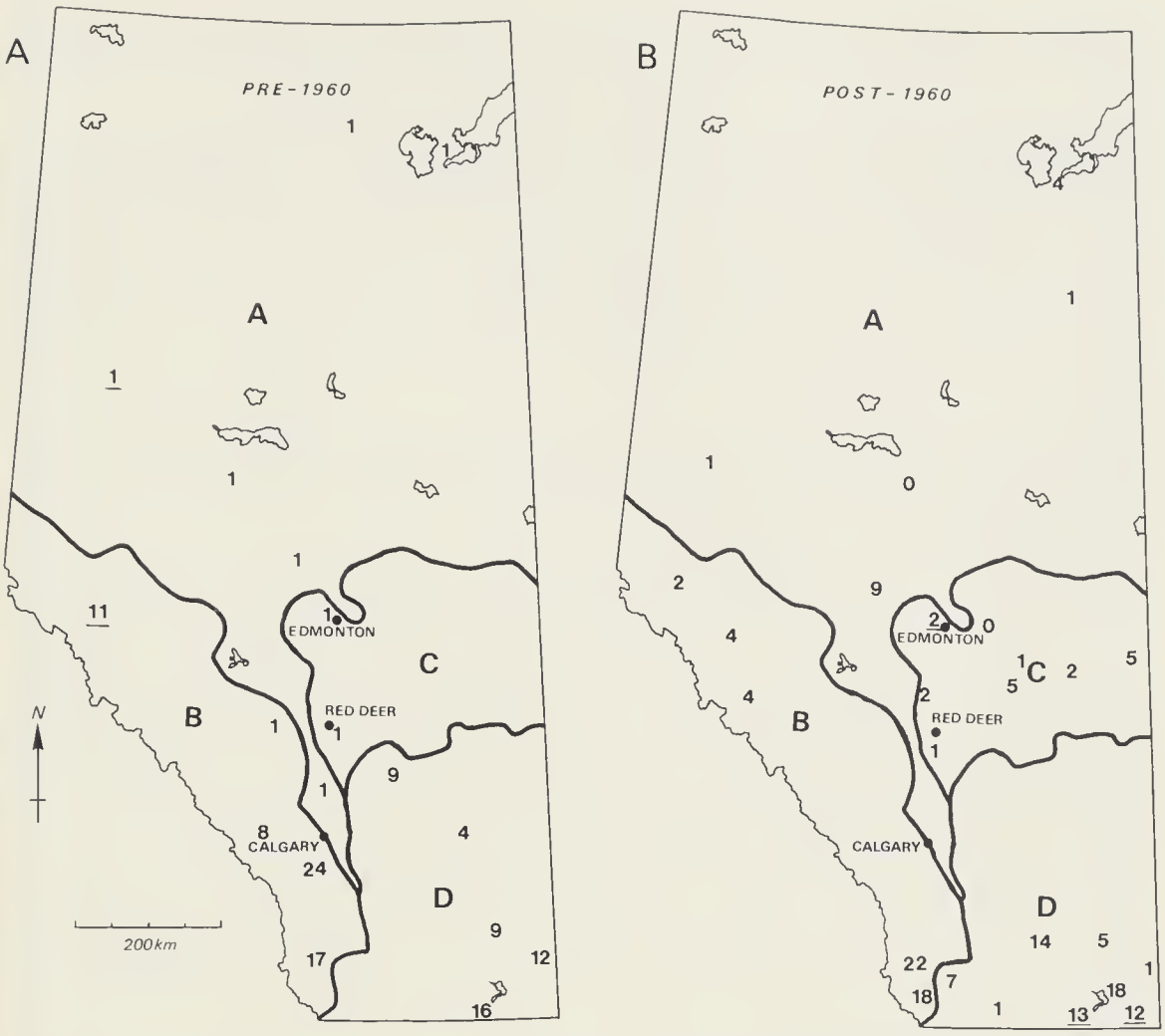

FIG. 1. Mean hybrid index scores of Northern Flicker specimens collected (A) prior to 1960, and (B) after 1960. Underlined values denote localities where five or more specimens have been obtained. Habitat zones are marked by letters: A—Boreal forest, B—Montane (includes foothills), C—Aspen parkland, and D—Grassland.

Of the 54 specimens that had been collected prior to 1960, flickers with intermediate or strong *cafer* characteristics generally occurred only in the Rocky Mountains and in southern Alberta, south of Red Deer (Fig. 1A). These two areas formed the primary area of hybridization between the two subspecies, with only one "pure" *cafer* (a female from near Calgary) and two "pure" *auratus* (a male and a female from near Red Deer) collected. As Short (1965) concluded, north of Red Deer a massive *auratus* population showed little or no effects of hybridization with *cafer* individuals.

Forty-four specimens collected subsequent to 1960 suggest that the *cafer* population is beginning to influence the northern *auratus* population (Fig. 1B). Several specimens collected north of Red Deer scored greater than 2 on the hybrid index (the highest score attained in specimens collected in this area prior to 1960). Of particular interest are two males collected in Whitecourt (160 km NW of Edmonton) and at Fort Chipewyan (600 km NE of Edmonton), respectively. The Whitecourt male (score = 9, National Museum of Canada 52900) had a brown crown with a gray hind neck, traces of gray in its ear coverts, mixed throat color, and traces of a nuchal patch. The Fort Chipewyan bird (score = 4, Prov. Mus. Alberta 80.64.149) had an intermediate crown color and red and black malar feathers in about equal

proportions. These specimens, and the significantly ($t = 2.11$, $P < 0.05$, N = 34) higher hybrid scores obtained from birds north of Red Deer and east of the mountains in the post-1960 sample ($\bar{x} = 2.00$, N = 19) compared to the pre-1960 sample ($\bar{x} = 0.77$, N = 17) suggest that *cafer* characteristics are spreading into the northern *auratus* population.

As Moore and Buchanan (1985) found in the U.S. Great Plains, we find that flicker hybrid scores are unchanged in the grasslands of southern Alberta. In the Rocky Mountain regions there is no evidence of change, but recent material is lacking from the northern Rockies because collecting is prohibited in the National Parks in that region. The areas of greatest change are the aspen parkland of east-central Alberta and the mixed forest to the north where *cafer* characteristics are more evident in the post-1960 sample than in the pre-1960 sample.

Expanding the pre-1960 sample from 22 (Short 1965) to 54 produced no substantive change in the boundaries of the hybrid flicker zone, and the post-1960 movement of *cafer* characteristics into the northern (above Red Deer) *auratus* population should not be dismissed as a artifact of increased sampling effort.

Unfortunately, there is no obvious explanation for recent changes in the flicker hybrid zone. If secondary contact was established as long ago as 10,000 years (Moore and Buchanan 1985, but see Rising 1983:151), there has been ample time for introgression of *cafer* genes into the northern *auratus* population. However, in the last 20 years, increased logging and clearing of pine forests along the northern foothills has produced more open habitat, perhaps facilitating movement of *cafer* into the northern parkland. In summary, the boundary between the northern *auratus* and western *cafer* flickers appears to be changing in central Alberta. The movement of *cafer* characteristics into the northern *auratus* area appears quite recent and should allow for an examination of the process of secondary contact.

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Breeding biology and nestling development of Golden-crowned Sparrows in Alaska.—Although substantial literature is available on the breeding biology of crowned sparrows (*Zonotrichia*), particularly the White-crowned Sparrow (*Z. leucophrys*) (cf. Morton 1976), little is known of the breeding and developmental biology of the Golden-crowned Sparrow (*Z. atricapilla*) (Kelly 1968, Verner and Willson 1969, Harrison 1978, Harrison 1979). Here I report on several aspects of the breeding biology of the latter species.

Study site and methods.—The study was conducted during June and July 1986 within an 8-km radius of Cold Bay, Alaska (55°12′N, 162°43′W), at about 20-m elevation near the tip of the Alaska Peninsula. This portion of the peninsula is maritime tundra, with patches of alders (*Alnus crispa*) and willow (*Salix* spp.) on slopes and along stream courses. For a more detailed description see Bailey (1974). The Golden-crowned Sparrow is a locally common to abundant breeder in southcoastal, southwestern, and western Alaska (Kessel and Gibson 1978), breeding as far west as suitable shrubby habitat exists (i.e., to Unimak Island in the Aleutian Islands about 50 km W of Cold Bay). Thus, my observations were near the western limit of the species' breeding range.

I observed 3 nests, which were visited daily when possible. I timed parental activities with a stopwatch. I did not capture or mark adults, but determined sex on the basis of differences in color of head markings (Mailliard 1932). Only the duller marked birds (presumed females) incubated and brooded, and only the birds with brighter yellow crowns and blacker head stripes (presumed males) sang. Nestlings were weighed daily (usually during a 2–3 h period around midday) to the nearest 0.1 g using a Pesola 30-g spring balance; body measurements were recorded to the nearest mm with a ruler. Nestlings were banded with U.S. Fish and Wildlife Service aluminum bands. Nestling growth rates were calculated as described by Ricklefs (1967). Significance level of statistical comparisons was set at $P \leq 0.05$.

Nest building and egg laying.—All 3 nests were cups of fine grass stems set in depressions in the ground and overhung by surrounding vegetation. Due to the nature of the overhanging vegetation, each nest had a definite entrance orientation. Nest 1 faced ENE and was in a patch of 0.8-m tall salmonberry (*Rubus spectabilis*). Nest 2 faced NW and was in a patch of 1-m tall willow. Nest 3 faced SSW and was under a small clump of 0.25-m tall lupine (*Lupinus* sp.) about 1 m from a patch of alder. Only nest 1 was discovered prior to egg laying. The nest was a well-formed cup on 4 June, with the final lining of ptarmigan feathers added on 6 June. The first egg was laid on 7 June, followed by 1 egg laid daily until the clutch of 5 eggs was completed. During this time the male sang frequently from several perches up to 75 m from the nest, but once the clutch was completed, his singing nearly ceased for the remainder of the nesting cycle. The clutch of nest 2 had 4 eggs. The clutch size of nest 3 could not be determined because I did not find it until the 5 nestlings were well feathered.

Incubation period.—The incubation period could be determined only for nest 1. Incubation began the day the last egg was laid (11 June), and 4 of 5 eggs hatched by the morning of 23 June. The last egg hatched by the following morning. Incubation lasted 12–12.5 days. Three of 4 eggs from nest 2 hatched by the morning of 25 June, and the last egg hatched by the morning of the following day.

During 5 h of observation, made over the 5 days prior to hatching from a hidden position 30 m from the nest, female 1 incubated 72% of the time (43 of 60 checks made at 5-min intervals). She flushed from the nest only when I approached to within 3 m.

Nestling period and nestling development.—At nest 1, 2 nestlings left the nest on 1 July, and the remaining 3 departed after I weighed them on 2 July. Only 2 nestlings remained in

TABLE 1

MEASUREMENTS OF GOLDEN-CROWNED SPARROW NESTLINGS NEAR COLD BAY, ALASKA

Age (days)	Weight (g)	Tarsus (mm)	Manus (mm)	Primaries (mm)[a]	Rectrices (mm)
0	3.0 ± 0.3 (7)[b]	5.0 ± 0.0 (7)	6.9 ± 0.4 (7)	—	—
1	5.1 ± 0.8 (9)	7.0 ± 0.7 (9)	8.2 ± 0.9 (9)	—	—
2	8.2 ± 1.0 (9)	9.7 ± 1.1 (9)	10.4 ± 0.8 (9)	—	—
3	11.4 ± 1.1 (9)	11.9 ± 1.1 (9)	12.6 ± 1.1 (9)	2.5 ± 0.9 (4)	—
4	15.6 ± 1.3 (9)	15.4 ± 1.5 (9)	15.8 ± 1.2 (9)	4.8 ± 1.8 (9)	—
5	19.7 ± 1.4 (9)	17.8 ± 0.9 (9)	18.0 ± 0.9 (9)	9.2 ± 2.3 (9)	1.7 ± 0.5 (3)
6	22.8 ± 1.1 (9)	19.7 ± 0.8 (9)	19.7 ± 0.9 (9)	14.6 ± 2.2 (9)	4.0 ± 1.9 (9)
7	24.0 ± 1.2 (9)	21.9 ± 0.3 (9)	21.0 ± 0.7 (9)	18.8 ± 6.9 (9)	7.8 ± 1.7 (9)
8	24.4 ± 1.4 (7)	22.0 ± 0.0 (7)	22.0 ± 0.0 (7)	29.4 ± 3.4 (7)	11.3 ± 0.5 (7)
9	23.1 ± 1.8 (5)	22.0 ± 0.0 (5)	22.0 ± 0.0 (5)	33.0 ± 3.2 (5)	13.2 ± 1.6 (5)

[a] Longest primary.
[b] $\bar{x}$ ± SD (N).

nest 2 on 4 July, and none was there the next day. The nestling period was about 9.5–10.5 days, although this is probably artificially short because I handled the young daily. Nestlings from nest 3, which was found on 10 July, left the nest on 12 and 13 July.

Nestlings reached 99% of fledging weight, 90% of fledging tarsus and manus length, and 44% of fledging primary (remiges) growth by day 6 (Table 1). The observed pattern of growth is best described by the logistic equation (see Ricklefs 1967). Assuming an asymptotic weight of 26.0 g (based on the last 2 nestlings in nest 3, which weighed 27.0 and 25.1 g on the day prior to their leaving the nest), the specific growth rate constant (K), which measures growth rate relative to the asymptote, was 0.632, with an inflection point at 4.4 days. The asymptote is about 82% of average adult weight (adults from British Columbia and Alaska in May to July had a mean weight of 31.8 g [N = 21]). The instantaneous growth rate at the inflection point (Ka/4) was 4.1 g/day.

On the hatch date, Golden-crowned Sparrows were 0.3–0.6 g heavier than White-crowned Sparrows (King and Hubbard 1981). A comparison of hatching weights of these two species from Alaska shows that the difference is significant ($t = 2.152$, df = 70, $P < 0.05$).

The following description of nestling development is a composite based on all individuals from all 3 nests. On hatching day (day 0), sparse gray down was about 15 mm long in the capital, spinal (on back only), humeral, femoral, and alar tracts. Eyes were closed and the nestlings gaped silently. Mouth lining was uniformly red, surrounded by a yellow rim on the beak. On day 2, all but the crural and ventral tracts darkened under the skin. When begging, nestlings did not vocalize, but some "peeped" faintly when handled. On day 3, eyes were beginning to open, the tips of primary pin feathers were beginning to penetrate the skin of some chicks, and the crural and anterior portions of their ventral tracts (to the breast region) were darkening under the skin. On day 4, gaping began to be accompanied by faint "peeps," eyes were almost fully open, and all tracts had pin feathers emerging. On day 5, nestlings oriented and gaped towards the nest entrance. No fear reaction was evident when they were handled. Feather tips were beginning to split in ventral, humeral, crural, and spinal tracts. By day 7, unhandled nestlings crouched silently and did not gape; one attempted to hop away. Pin feathers in all tracts were splitting. On day 8, several nestlings jumped from nests after crouching and being handled. On day 9, some nestlings gave a

harsh distress call and struggled when handled. All could stand and perch without difficulty but were still flightless and remained so until after leaving the nest.

Parental activities during nestling period.—Female 1 brooded her nestlings at least until 30 June (2 days prior to nest departure). In 5 h of observation during the nestling period, the proportion of time spent by the female brooding ranged from 67% (8 of 12 5-min checks) on 23 June to 17% (2 of 12 5-min checks) on 27 and 30 June. She was not seen brooding thereafter. Female 2 was flushed from her nest on 25 and 26 June, but not after that date (N = 8 checks to fledging). Males were never flushed from nests, nor were they seen to brood.

Both sexes fed nestlings and removed fecal sacs. During 3 h of observation at nest 1 (over the 3 days prior to fledging), the male delivered food 5 times but removed no fecal sacs. Female 1 made 39 deliveries and removed 4 fecal sacs. During 2.75 h of observation at nest 3 (over the 2 days prior to fledging), the male made 12 food deliveries and removed 4 fecal sacs; the female made 9 food deliveries and removed 1 fecal sac. Recognizable foods delivered to nestlings included lepidopteran larvae, an adult butterfly (*Pieris napi*), adult craneflies (Diptera: Tipulidae), and adult stoneflies (Plecoptera).

Postfledging dispersal.—Two of the young from nest 1 were captured on 5 July, 2 and 3 days after leaving the nest. The two fledglings were 75 m and 80 m from the nest, respectively. They were 50 m apart and capable of short flights, and tried to escape by hiding. Both adults fed both nestlings.

Discussion.—My data indicate a close similarity between the incubation periods of Golden-crowned and White-crowned sparrows (King and Hubbard 1981). The age of fledging of Golden-crowned Sparrows is more like that of southern White-crowned Sparrows than that of the more northern populations. The greatest difference in fledging age is with the Alaska White-crowned Sparrow populations (see King and Hubbard 1981), in which nestlings fledge 8.0–9.0 days after they hatch. In part, this difference in fledging age is probably a function of the larger body size of Golden-crowned Sparrow nestlings (19–20 g at fledging for White-crowned Sparrows vs at least 23–24 g for Golden-crowned Sparrows). Development of nestling Golden-crowned Sparrows is also similar to that of White-crowned Sparrows (Morton et al. 1972, King and Hubbard 1981), although the growth rate constant (K) of Golden-crowned Sparrows is larger.

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Caching by Red-breasted Nuthatches.—The Red-breasted Nuthatch (*Sitta canadensis*) breeds in boreal forests and erupts southward in winters when its normal food of conifer seeds is in short supply (Larson and Bock 1986). Roberts (1979) remarked that caching is undocumented in such eruptive individuals far from their coniferous forest breeding areas. During the winter of 1985–86, we studied "copying" of food-finding (Krebs 1973) by free-ranging birds of a bark-foraging guild in Ohio. Although Red-breasted Nuthatches are usually absent from the deciduous woodlands of our study area, we encountered the species during a replicate of an experiment (described elsewhere) when three individuals provided us with evidence that caching occurs in birds wintering outside the breeding range.

We made available to color-marked birds of mixed-species foraging flocks a supply of mealworms (*Tenebrio* sp.) hidden in a hollow sapling. The mealworms could be extracted only through a small inconspicuous hole. Dominance relationships within and across species were determined from records of chases and supplanting attacks (Hinde 1952).

Mealworms were taken by three Red-breasted Nuthatches between 09:48 on 31 January and 08:36 on 1 February (Fig. 1). For comparative purposes, we also show the record of mealworms taken by the dominant pair of Carolina Chickadees (*Parus carolinensis*) in the same flock. Carolina Chickadees did not cache mealworms during any of our observations. We confined our analysis of caching to the period between 11:36 and 16:00 on 31 January, when all three nutchatches and both chickadees were removing mealworms. At 11:36, air temperature in the shade was −3.0°C, wind velocity 1 m above the ground was 0.7 m sec^{-1}, direct solar radiation was 8 mW cm^{-2}, and snow depth was 8 cm.

Although we were able to observe the nuthatches caching mealworms in neighboring trees periodically throughout the day, we concentrated most of our attention on the food source

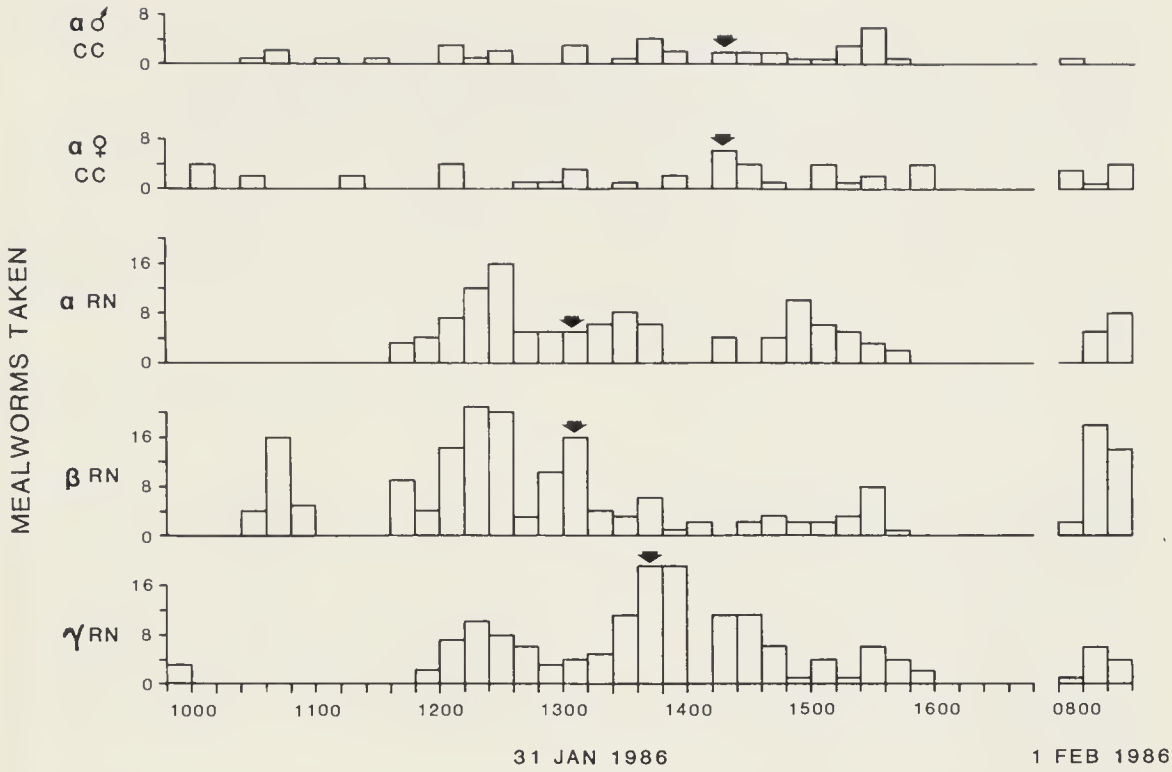

FIG. 1. Mealworms taken from a feeder by 2 Carolina Chickadees (CC) and 3 Red-breasted Nuthatches (RN) on 31 January and 1 February 1986. Medians denoted by arrows in the figure used records from the period between 11:36 and 16:00 on 31 January.

to record the identity of all birds taking mealworms. Thus, we assume that had they not been caching, the nuthatches would have consumed mealworms at about the same rate as the two chickadees. This assumption seems reasonable because the nuthatches (12.0, 11.9, 11.4 g) were similar in mass to the chickadees (10.8, 10.3 g) and, therefore presumably, in metabolic requirements. Although it is true that the act of caching must have involved some additional metabolic cost, we have insufficient data to approximate what that increase might have been. We assume that all mealworms removed by nuthatches over and above the number removed by the chickadees were cached, but we recognize that some of the additional mealworms may have been eaten rather than cached.

During the 22 12-min periods between 11:36 and 16:00 that we oberved the birds, the two chickadees took 36 and 34 mealworms, respectively, while the alpha (male), beta (female), and gamma (male) individuals in the intraspecific dominance hierarchy among the nuthatches removed 107, 186, and 140 mealworms, respectively. The difference between the two species in removal of mealworms was significant (two-tailed t-test; $P < 0.05$). Although number of mealworms taken per 12-min period was significantly correlated for the alpha and beta nuthatches (Pearson's $r = 0.69$; $P < 0.05$), correlations between each of these birds and the gamma nuthatch were nonsignificant (Pearson's $r = 0.06$ and 0.05, respectively). The alpha and beta birds each took half the day's total of mealworms by 13:12, but the gamma nuthatch did not take half its mealworms until 13:48.

Assuming that each nuthatch consumed 35 mealworms during the period (the average for the chickadees) the alpha, beta, and gamma nuthatches, respectively, cached 72, 151, and 105 mealworms in the surrounding woods. These totals amount to a mealworm being cached every 3.7, 1.8, and 2.5 min, respectively, for the three birds throughout the 4.4-h

period of analysis. The 1.9-cm-long mealworms averaged 0.86 kcal in energy content (Waite 1986). Therefore, the alpha, beta, and gamma nuthatches cached approximately 61.9, 129.9, and 90.3 kcal, respectively, during the period, or 14.1, 29.5, and 20.5 kcal h^{-1}.

These results circumstantially demonstrate a strong tendency for Red-breasted Nuthatches to cache food at a site outside the breeding range. The waning of caching late in the day—shown most clearly by the alpha and beta birds—is consistent with the hypothesis that items of food cached early in the day are retrieved and eaten later on the same day during the hyperphagia accompanying fat deposition (Sherry 1985). Throughout the day, the alpha nuthatch attempted to defend the food source against chickadees and the other Red-breasted Nuthatches. Time devoted to chasing and display may have caused the reduction in this bird's caching below the levels shown by the beta and gamma birds. Any caching rhythm in this species, however, appears subject to modification by proximate circumstances as shown by the gamma bird which cached later in the day than during the most intensive caching period of its dominant conspecifics.

Caching behavior has been shown to be intense in Red-breasted, White-breasted ([*Sitta carolinensis*]; Waite and Grubb, in press), and European ([*Sitta europaea*]; Moreno et al. 1981, B. Enoksson, pers. comm.) nuthatches. As nuthatches adapt readily to life in captivity (Pierce and Grubb 1981; Waite and Grubb, in press), the caching behavior of *Sitta* could be a useful tool for testing models of caching patterns (Stapanian and Smith 1978, Clarkson et al. 1986), memory for locations of caches (Kamil and Balda 1985), and timing of the retrieval of caches (Stevens and Krebs 1986).

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Age-class differences in the use of food sources by European Starlings.—The foraging patterns of adult birds often differ from those of juvenile conspecifics. Such age-class differences may be related to the juveniles' lack of skill at a difficult foraging technique (e.g., plunge-diving; Dunn 1972), adult-juvenile competition (Burger and Gochfeld 1983), or because juveniles forage in areas that contain little food (Magrath and Lill 1985).

Age-specific diet differences occur in European Starlings (*Sturnus vulgaris*). While adults continue to feed on soil invertebrates through the summer (Tinbergen 1981), the diet of fully independent juveniles consists largely of plant matter (Feare 1984). Juveniles are less able than adults to locate soil invertebrates (Stevens 1985). The segregation of age classes into different foraging habitats appears to occur only in summer (Feare 1984).

Here I (1) compare the foraging substrates used by adult and recently fledged juvenile starlings during two breeding seasons, (2) present evidence that the food sources used by juveniles often are of poor quality, and (3) speculate that the latter may contribute to the high juvenile mortality during this time of year (Coulson 1960).

Study areas.—I established two circular 300-km^2 study areas in central New Jersey. Owing to the starling's broad diet (Lindsey 1939), I selected two study areas with different land-use characteristics. The Franklin area, near New Brunswick in Middlesex County, was mostly urban-suburban, with abundant grassland but little agriculture. The Adelphia area, 40 km SSE of Franklin in Monmouth County, was largely rural-agricultural, with less grassland than Franklin.

Methods.—I estimated starling populations during weekly roadside censuses along 50 km of established routes in each study area during the breeding seasons of 1983 and 1984. Censuses were begun within 30 min after sunrise and lasted about 3 h. I drove at an average speed of 30 km/h, and stopped often to observe birds. Foraging birds were recorded as adult or juvenile, and each was assigned a foraging substrate, including grassland (managed lawns; unmanaged pastures and meadows); crop fields (mainly soybean, corn, and small grain) in various stages (plowed, planted, mature, harvested, fallow), and human-assisted sources (e.g., bird feeders, garbage pails). I did not assign an age class to flying or resting birds. Censuses began in early June, after first-brood juveniles were observed in the area, and were discontinued in early August after I could no longer use plumage to separate juvenile from adult birds with sufficient reliability. Each two consecutive weekly censuses were combined into biweekly periods to facilitate comparisons with food availability, which was measured every two weeks.

I measured invertebrate density in grassland and growing soybean fields, and grain density in harvested wheat fields. In each study area I sampled three grass fields and three fields of both crop types every two weeks. Grasses were sampled using a grid technique (Ng et al. 1983). The surface, thatch, and soil were searched to a depth of 4 cm, which I judged to be

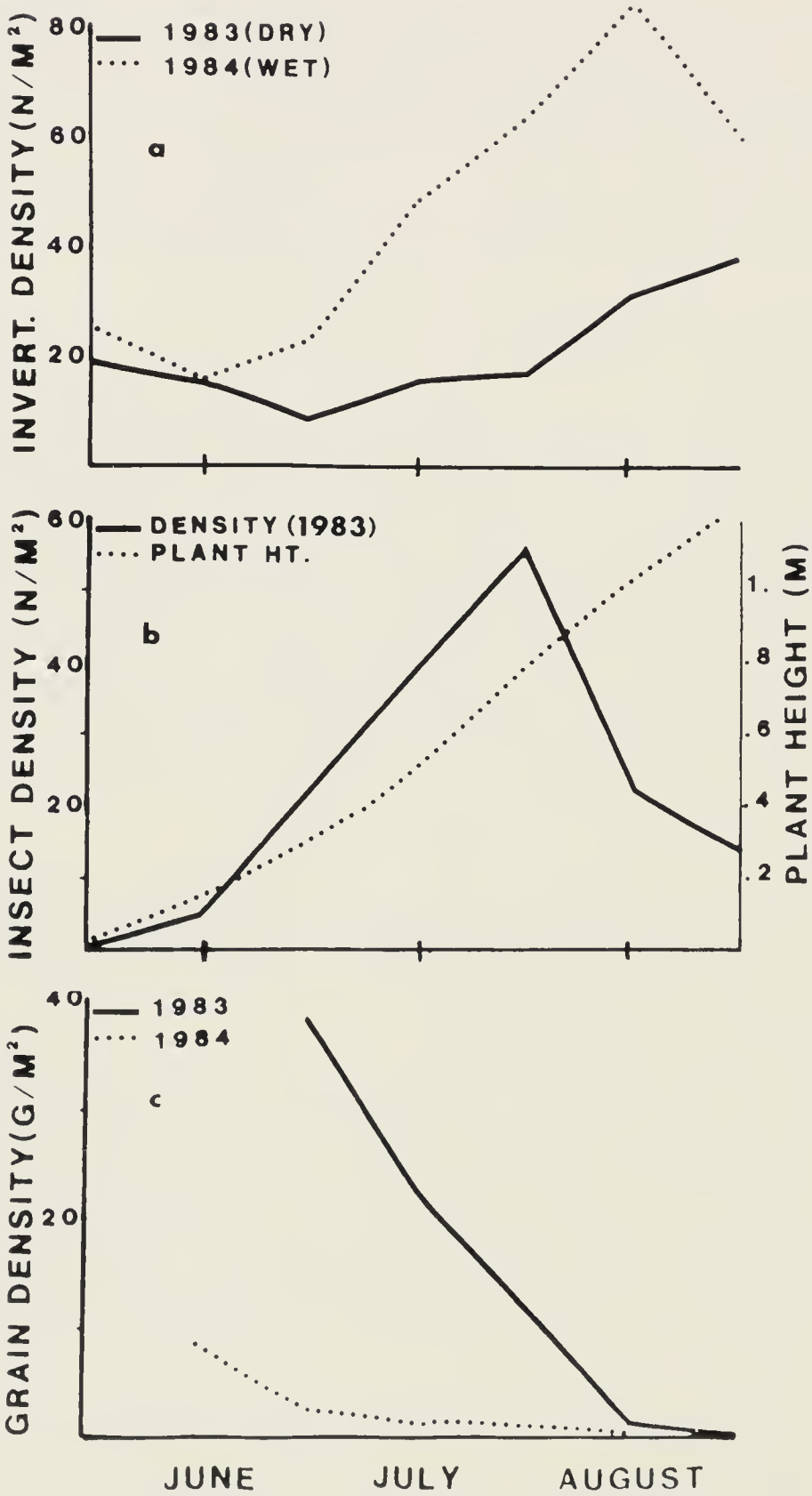

FIG. 1. (A) Total invertebrate density in grasses in 1983 and 1984. (B) Insect density in growing soybean fields in 1983. (Density was estimated to be about half as great in 1984 because of wet soil.) (C) Grain density in harvested wheat fields in 1983 and 1984. (Figures based on 6 grass fields and 6 fields of both crop types sampled every 2 weeks.)

TABLE 1

TOTAL ADULT AND JUVENILE FORAGING POPULATIONS DURING SIX BIWEEKLY PERIODS IN 1983 AND 1984 (FIGURES IN PARENTHESES ARE PERCENTAGES)

	1983			1984		
Age class	Franklin	Adelphia	Total	Franklin	Adelphia	Total
Adults	4940 (83)	5766 (69)	10,706 (75)	3686 (71)	3354 (70)	7040 (71)
Juveniles	1010 (17)	2591 (31)	3601 (25)	1506 (29)	1438 (30)	2944 (29)
Total	5950 (42)	8357 (58)	14,307	5192 (52)	4792 (48)	9984

the maximum probe depth of starlings. Samples were taken early in the morning before invertebrates had moved deeper to avoid desiccation. Insect density on soybean plants was measured using a direct-observation method (Mayse et al. 1978). In addition, a 100-cm^2 area near the base of each sampled plant was inspected to a depth of 4 cm for soil dwelling invertebrates. In both grassland and soybean fields, only invertebrates >4 mm were included in density estimates. I used a modified grid technique to measure grain density in harvested wheat fields (Ng et al. 1983).

Results.—Coleoptera (44%), mainly larvae, and earthworms (39%) were the most common grassland invertebrates. Total invertebrate density (TID) was lower in 1983, a dry summer (20 ± 9 individuals/m^2 [SD]), than in 1984, a wetter summer (44 ± 25 individuals/m^2) ($t = 2.87$, df = 22, $P < 0.01$) (Fig. 1A).

Although plant insects were not common in soybean fields (maximum 0.3 insects/plant), small (<5 mm) adult soil-dwelling beetles (mainly Chrysomelidae) were abundant. In 1983, total density increased from 6 ± 3 insects/m^2 in early June to 56 ± 32 insects/m^2 by mid-August (Fig. 1B). Owing to rain-soaked fields in 1984, insect density declined by about half between years.

In 1983, grain density in harvested wheat fields fell from 39 ± 10 g/m^2 in mid-July to 12 ± 5 g/m^2 in mid-August (Fig. 1C). Heavy spring rains in 1984 resulted in a substantial loss of the wheat crop. About half of all fields were plowed under before harvest; in undamaged fields, the harvest period was shorter and began about three weeks earlier than in 1983. In 1984 grain density declined from 8 ± 6 g/m^2 in late June to <1 g/m^2 by late July.

Starling populations.—Birds could be aged by plumage during six biweekly periods each year. In 1983, both the total number of birds and the number of juveniles were higher in Adelphia than in Franklin ($\chi^2 = 60.2$, df = 1, $P < 0.001$). In 1984, neither the total number of birds nor the number of juveniles differed significantly between study areas (Table 1).

Adults and juveniles used available foraging substrates differently ($\chi^2 = 415.7$ in 1983 and 293.7 in 1984, df = 5, $P < 0.001$) (Table 2). Adults were more numerous than expected in managed grassland both years, and they were more abundant than expected at human-assisted food sources in 1984; aggression by adults often restricted juvenile access to these sources (unpubl. data). Juveniles were more numerous than expected in unmanaged grassland, and in soybean and wheat fields both years, and in agricultural fields other than soybean and wheat in 1984.

Between years, proportionate use of unmanaged grassland by adults decreased significantly, whereas the use of agricultural fields other than soybean and wheat increased significantly.

TABLE 2

NUMBER OF ADULT AND JUVENILE STARLINGS USING VARIOUS FORAGING SUBSTRATES EACH BIWEEKLY PERIOD IN 1983 AND 1984 (FIGURES IN PARENTHESES ARE PERCENTAGES)

Substrate	1983			1984		
	Adults	Jvnles	Total	Adults	Jvnles	Total
Managed grasses	929[a]	119	1048	652[a]	125	777
	(61)	(21)	(50)	(60)	(22)	(47)
Unmanaged grasses	252	124[a]	376	97	118[a]	215[b]
	(16)	(22)	(18)	(9)	(21)	(13)
Growing soybean	60	146[a]	206	62	104[a]	166
	(4)	(26)	(10)	(5)	(18)	(10)
Harvested wheat	76	98[a]	174	46	45[a]	91[b]
	(5)	(18)	(8)	(4)	(8)	(5)
All other agriculture	93	34	127	126	152[a]	278[b]
	(6)	(6)	(6)	(12)	(26)	(17)
Human-assisted	119	38	157	112[a]	25	137
	(8)	(7)	(8)	(10)	(5)	(8)
Total	1529	559	2088	1095	569	1664

[a] $P < 0.001$, indicates significant overrepresentation by an age class, determined by Chi-square analysis of foraging population.

[b] $P < 0.001$, indicates significant proportionate increase or decrease between 1983 and 1984, determined by Chi-square analysis.

For juveniles, there was a significant decrease between years in proportionate use of both soybean and wheat fields, whereas use of other agricultural fields increased significantly (Table 2).

Wheat fields, soybean fields, and grassland together accounted for 88% and 84% of all foraging birds in Franklin and Adelphia, respectively. Neither age class used harvested wheat fields in proportion to grain density. The use of growing soybean fields by juveniles was correlated significantly with insect density at these sites ($r = 0.59$, df = 18, $P < 0.01$), but there was no relationship between insect abundance and use of soybean fields by adults. Use of grassland by adults was correlated negatively with TID in 1983 ($r = -0.64$, df = 10, $P < 0.02$), but positively with TID in 1984 ($r = 0.63$, df = 10, $P < 0.02$). Juveniles foraged in grassland independent of TID both years.

Discussion.—Segregation of adult and juvenile starlings into different foraging habitats followed a similar pattern in both years, despite differences between years in food availability and distribution. Segregation by age class was extreme in grassland. Adults, which used managed grassland extensively both years (61% and 60%) despite a two-fold increase between years in prey density, presumably are able to locate scarce soil-dwelling invertebrates. Adults may use managed grassland because it provides invertebrates required by nestlings (Tinbergen 1981). Morrison and Caccamise (1985) found that even after the breeding season, individual starlings show strong fidelity to such areas. Familiarity with an area might increase an individual's foraging efficiency in that area.

In contrast, juveniles were uncommon on managed grassland. Recently fledged juveniles are probably less efficient than adults at probing for soil-dwelling invertebrates (Feare 1984).

Juveniles in the present study used grassland irrespective of invertebrate density both years, which suggests they may also be poor at assessing prey availability. Juveniles, however, were not tied to grassland as were adults, and they foraged widely in crop fields. Grain lying on the surface of wheat fields, and insects in the soft, bare soil of crop fields probably can be found with little skill. Juveniles also may reduce direct competition with adults on managed grassland by using agricultural fields and unmanaged grassland, in which adults were less common.

The foraging substrates used by juveniles often were of low quality. For example, the pastures used extensively by juveniles typically were large, unmanaged fields in which the grass was higher than that on the lawns used by adults. Starlings have lower capture success in taller grass (Brownsmith 1977), and may be less able to detect both conspecifics and potential predators when feeding in these areas. In addition, owing to rapid depletion, little grain remained in wheat fields by mid-summer, when use of these fields by juveniles peaked. Although insect abundance in soybean fields increased through August, these fields were used by juveniles only until plants reached approximately 60 cm, in July, perhaps because above this height their vision is obscured.

Recently fledged starlings may achieve poor foraging success because of low grain abundance, poor accessibility of tall-grass invertebrates, and competition with adults for human-assisted food sources and, perhaps, invertebrates in managed grassland. Juvenile mortality, which appears to be highest during summer (Coulson 1960), may, in part, be due to such competition as well as other characteristics of the food supply.

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Standard rate of metabolism in the Common Barn-Owl (*Tyto alba*).—A number of studies have examined metabolic rates of owl species in relation to ambient temperature (Graber 1962, Ligon 1969, Coulombe 1970, Gessaman 1972). None, however, has examined standard metabolic rates for any member of the family Tytonidae. Here I present results from a series of measurements estimating the standard metabolic rate of the Common Barn-Owl (*Tyto alba*).

Two adult Common Barn-Owls were obtained from the Center for Birds of Prey, Florida Audubon Society, Maitland, Florida, and housed in an indoor aviary at the University of Florida. Aviary temperature was approximately 25°C. Birds were fed a diet of chicks and rats for 6 days and fasted on the seventh. All experiments were run with birds in a postabsorptive state. Because I was unable to obtain permission to laparotomize the birds, I identified sex by comparing each bird against 95% confidence intervals about mean male and female Common Barn-Owl weights (data from Earhart and Johnson 1970:table 2). Although some overlap in confidence intervals existed, weights of both birds used here (488.2, 578.2 g) were outside the male confidence interval and within that calculated for females.

Prior to each experiment, birds were weighed to the nearest 0.1 g, and body temperature (T_b; °C) was measured by placing a thermister probe into the cloaca. Birds were then placed in an open-system chamber approximately 5 liters in volume, and oxygen consumption measured with an Applied Electrochemistry Oxygen Analyzer (Model S3A). Soda lime and silica gel were used to remove carbon dioxide and water, respectively, from air exiting the chamber. Environmental temperatures were controlled by submersing the chamber containing a bird in a thermoregulated water bath. Oxygen consumption ($\dot{V}_{O_2}$; cm^3O_2/g-h) was calculated from a formula derived by Depocas and Hart (1957). Flow rates ranged from 0.35 to 0.75 liters/min (STPD). Multiple runs at different temperatures were made on each individual bird, and an experiment ended when oxygen consumption was steady for at least 30 min. All experiments were run during the daytime. Birds were weighed to the nearest 0.1 g and body temperature recorded immediately after each experiment. All values are presented as mean ± 1 SD unless indicated otherwise.

The thermoneutral zone (TNZ) of Common Barn-Owls extended from 22.5 to 32.5°C (Fig. 1). Mean oxygen consumption within this zone was 0.604 ± 0.051 cm^3O_2/g-h. This value is significantly greater ($P < 0.001$) than that predicted by Aschoff and Pohl's (1970) relationship for inactive nonpasserine birds, but within the range of values reported for Strigidae owls (Ligon 1969:table 1) and that predicted by Zar's relationship for strigiforms (1968). Below TNZ, $\dot{V}_{O_2}$ was explained by the relationship $1.161 - 0.024(T_a)$ ($r^2 = 0.90$, $P < 0.001$) and extrapolated to zero metabolism at 47.9°C. Body temperatures averaged 37.8 ± 0.6°C across the range of chamber temperatures (Fig. 1).

Use of the slope of the regression below TNZ as a measure of conductance is valid only if the line extrapolates to the mean T_b (McNab 1980). Because the line below TNZ extrapolates to a temperature greater than the mean T_b, it suggests that Common Barn-Owls

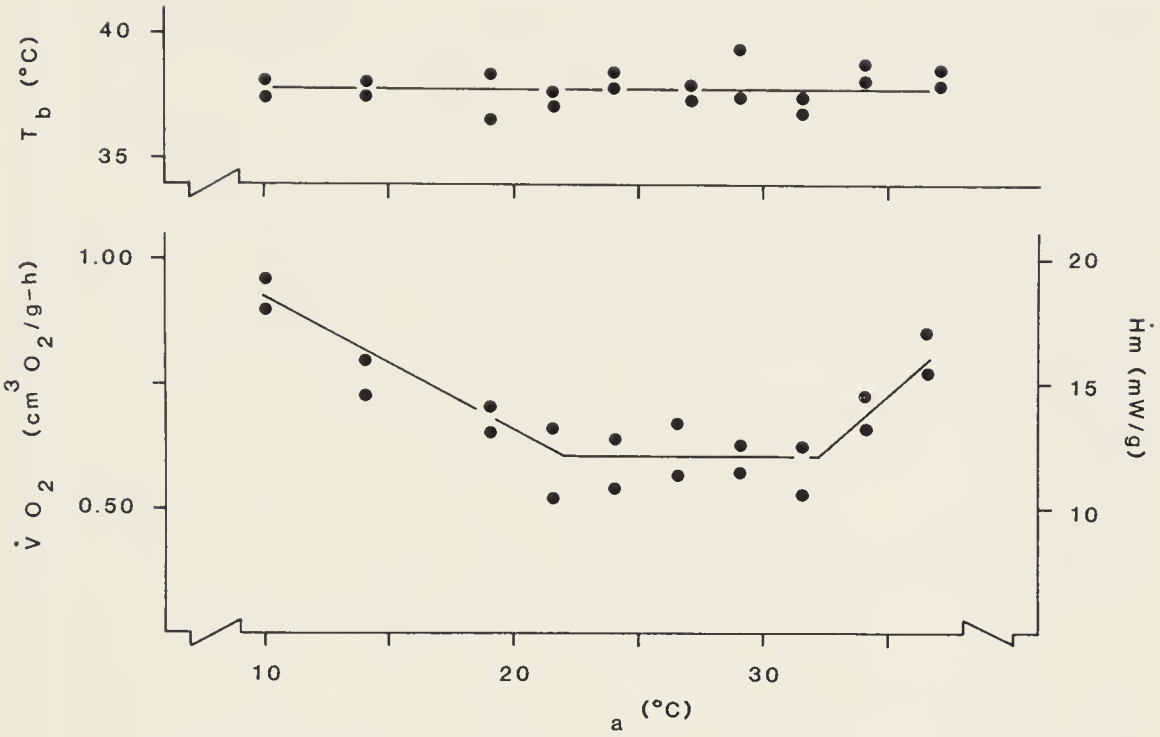

FIG. 1. Relation of body temperature (T_b), oxygen consumption ($\dot{V}_{O_2}$) and metabolic heat production (H_m) to environmental temperature (T_a). H_m was estimated by assuming 20.08 kJ heat produced per liter of O_2 consumed (after Hayworth and Weathers 1984).

respond to a decrease in T_a by increasing heat production and simultaneously decreasing conductance. A more accurate measure of conductance under these circumstances is obtained from the equation, $C = \dot{V}_{O_2}/(T_b - T_a)$, where C is conductance in cm^3O_2/g-h°C (McNab 1980). Mean minimal conductance calculated from this relationship was -0.037 ± 0.004 cm^3O_2/g-h°C, a significantly steeper ($P < 0.001$) slope than that generated by simple regression.

Oxygen consumption by Common Barn-Owls differs little from values reported for other owls. Whether or not metabolic rates of other owls in Tytonidae (e.g., Grey Sooty Owl [*T. tenebricosa*], Eastern Bay Owl [*Phodilus badius*]) constitute a cluster distinct from Strigidae owls is unknown, and can be determined only by further work.

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Vocalizations of female Red-winged Blackbirds inhibit sexual harassment.—Breeding female Red-winged Blaekbirds (*Agelaius phoeniceus*) are frequently vocal in the vicinity of their nests, where they typically utter chatter-like vocalizations when arriving and departing as well as while flying through their mates' territories. Beletsky and Orians (1985) identify these vocalizations as "Type 1" songs, thought to be used by females primarily for intrapair communication (Beletsky 1983). They suggest that the function of these vocalizations, when given around nests, is to identify females and their breeding statuses to their mates. One suggested benefit of frequent vocal identification in these situations is sexual noninterference by males, who regularly pursue, often for long distances, females that fly into their territories. If resident females were pursued in this manner, their abilities to build nests, ineubate, and feed nestlings could be impaired. Beletsky and Orians (1985) support this suggestion with data showing that female Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), which also usually vocalize when leaving and approaching their nests, are chased by their mates significantly more often if they depart silently than if they vocalize when leaving. Here we present similar data for Red-winged Blackbirds.

The breeding biology of Red-winged Blackbirds is described in detail by Orians and Christman (1968) and Orians (1980). Our observations were made during May 1986 at a marsh in the Columbia National Wildlife Refuge, Grant County, Washington. The marsh contained 12 territorial male Red-winged Blackbirds and more than 30 breeding females. All males and most females were eolor banded for individual identification. We observed female movements and male behavior from a 6-m high eliff overlooking the marsh. For each arrival at and departure from a nest, we recorded whether the female vocalized and whether she was chased by her mate. All females monitored during this study, and previously (Beletsky and Orians 1985), vocalized near their nests.

We observed 47 departures and 44 arrivals of females at their nests. More than 10 different females were observed. For all arrivals, females were returning from foraging off the territories of their mates. None of the departing females that vocalized was ehased (0/37), whereas 40% (4/10) of females departing silently were chased. Three pereent (1/33) of females that voealized while arriving were ehased, whereas 36% (4/11) of those arriving silently were

chased. Females departing or arriving silently were therefore chased significantly more often than those that vocalized ($\chi^2 = 11.45$, 1-tailed test, $P < 0.001$ and $\chi^2 = 6.09$, $P < 0.02$, respectively).

Our results suggest that these vocalizations decrease the probability that a female is chased and possibly diverted from nest-tending duties. Many females that were chased vocalized at some point during the chase, but because chases were so rapid and sometimes obscured by vegetation, we could not tell if males recognized the females when they vocalized and stopped chasing them. After being chased, females usually returned quickly to areas near their nests.

Given the large number of breeding females with which a territorial male interacts (up to a dozen on his own territory plus dozens of others on adjacent areas), selection for mechanisms that enable males to discriminate between those females potentially responsive to courtship and copulation and those females already engaged in nesting is likely. Males also should benefit by not chasing females it is not to their advantage to chase. Type 1 songs may also have the longer-term effect of promoting pairbonds during those nesting stages when direct contact between mates is infrequent, e.g., during incubation (Beletsky and Orians 1985).

Because in the majority of instances all females leaving and arriving at their nests vocalize (Beletsky and Orians 1985, pers. obs.), the observation that 20–25% of movements around nests are performed in silence may be revealing. Although females apparently vocalize in these situations regardless of the presence of their mates (Beletsky and Orians 1985), patterns and contexts of silent departures have not been studied. Silent flights that regularly elicit chasing when detected by mates or other males may provide females in relatively advanced nesting phases means of affecting male behavior. For example, earlier-nesting females may have interests in delaying breeding of later-arriving females in order to reduce competition in foraging or to monopolize male parental investment (Yasukawa and Searcy 1981, 1982). By mimicking strangers by flying silently, nesting females might elicit chasing, thus distracting their mates' attentions from other females.

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Relaying interval after nest failure in Gray Catbirds and Northern Cardinals.—Nest failures, followed by renesting, occur frequently among passerines. The rate at which a bird renests can affect its productivity by influencing the number of its nesting attempts (Ricklefs 1973, Finch 1984). Quick renesting need not increase the number of renesting attempts, as some individuals might renest only once a season. If renesting followed a failure quickly it would provide, however, a longer time to care for fledglings, should they be produced. Quick renesting would be particularly important in a species with a short laying season. For such a species, time saved in renesting would have a proportionately greater effect than would be so for a species with a long laying season.

We present extensive data on renesting following nest failure for two species that breed in the same macrohabitat at London, Ontario: the Gray Catbird (*Dumetella carolinensis*), a migrant species, and the Northern Cardinal (*Cardinalis cardinalis*), a resident species. At London, Ontario, the laying season of catbirds extends about 50 days between mid-May and early July (Darley et al. 1971), but that of cardinals is about 120 days from mid-April to mid-August (Scott 1963).

Here we (1) compare the length of the interval between nest failure and relaying between catbirds and cardinals, and (2) relate the length of this interval to the minimum time required for rapid yolk deposition in the development of a new clutch.

Methods.—We observed cardinal nests from 1955 to 1961, and catbird nests in 1963, 1964, and 1969. The data are those used by Scott and Ankney (1980:682) to support their argument that female passerines can quickly obtain nutrients for egg production. All replacement nests of catbirds, and about 75% of those of cardinals, belonged to uniquely color-marked females that were being studied on the campus of the University of Western Ontario, London, Ontario.

We recorded the time between a failed nest and its replacement as the number of days (interval) between the day on which we recorded nest failure and the day when the first egg was laid in the next nest. We visited most nests daily, presumably after the laying hour. Thus, the observed interval was about one-half day *shorter* than the actual interval because failure occurred sometime during the 24 h preceding observation of nest failure. Parenthetically, we wish to stress that some investigators have recorded the interval between the last day a nest was active and the day that the first replacement egg was laid. In these cases, the observed interval would be about one-half day *longer* than the actual interval between failure and relaying. Thus, the two ways of recording the interval would yield a difference of 1 day for a particular case.

About 10% of our visits were made at longer than a daily interval, and when nest failure occurred during 2 days between visits we estimated the day of nest failure as occurring on one or the other of 2 days. Such intervals have been plotted in Fig. 1 for the mid-point of the two possible intervals (e.g., if the interval was either 3 or 4 days it has been plotted as 3.5 days). In Table 1, such an interval has been indicated as 3–4 days.

We usually treated the first nest found after nest failure as the replacement. In two cases, however, one involving each species, each female built two nests simultaneously but laid in only one, which we regarded as the replacement nest. This unusual behavior caused two long intervals: 7 days for the catbird (the second longest recorded in this study) and 10 days for the cardinal. Unusually long intervals could have resulted, however, if we failed to find the first replacement nest. We excluded from analysis six intervals, ranging from 14 to 31 days, because we had no record of the activities of the birds during those periods and, thus, we could have missed earlier nests.

Two exceptionally short intervals of 3 days, in cardinals, although plotted in Fig. 1, have

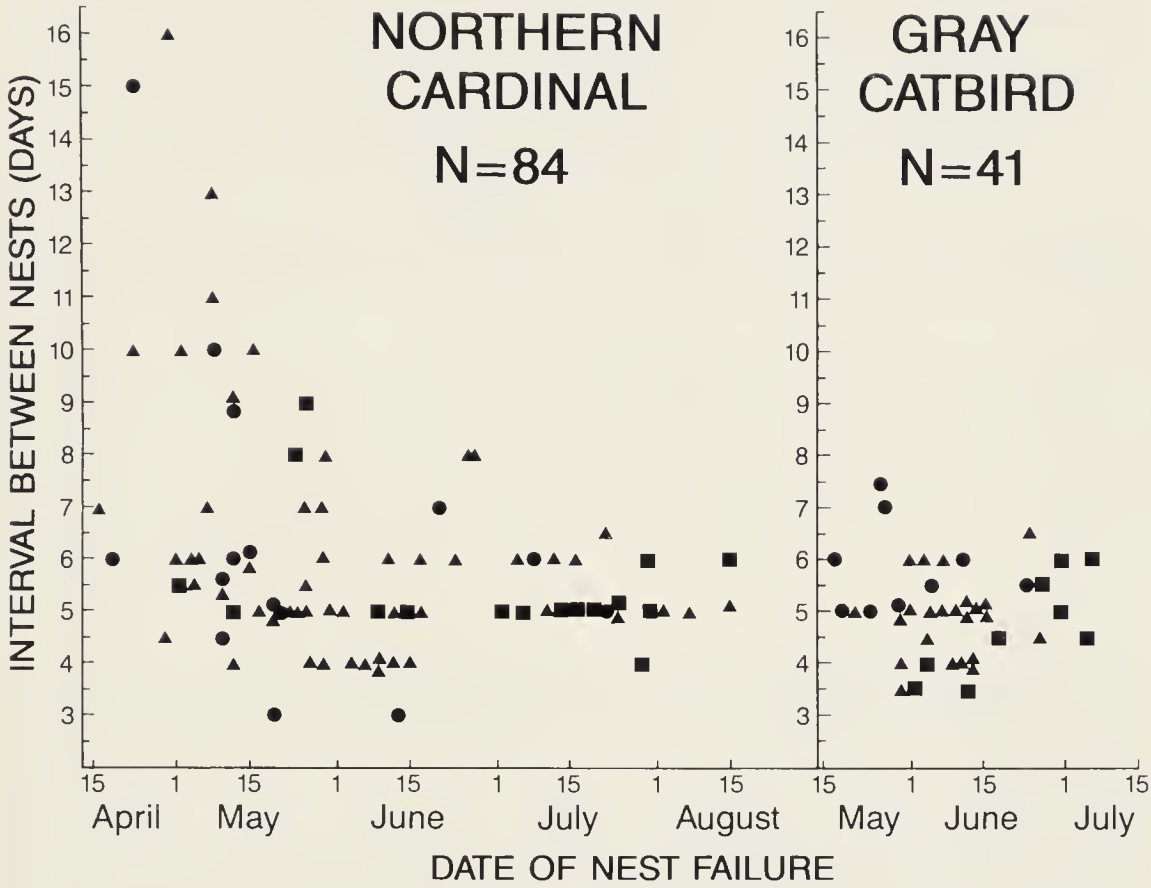

FIG. 1. Variation in the length of intervals between nest failure and first replacement egg by cardinals and catbirds. Stages of the nesting cycle when failure occurred are indicated by circles (laying), triangles (incubating), and squares (brooding).

been omitted from all analyses because they are not comparable with other intervals. Each 3-day interval followed the loss within a few hours of the only egg laid in that nest. As almost all cardinals here lay only 3 eggs, each of these two females on the day of nest failure almost certainly had one large yolky oocyte, unlike birds which lost nests later in the cycle.

We used meteorological summaries for London obtained from Environment Canada, Atmospheric Environment Service, in our analysis of a relationship between interval length and weather. Statistical procedures followed those of Sokal and Rohlf (1981).

Results.—During 17 May–6 July, when both species were laying, 41 catbirds renested 5.05 ± 0.92 days [SD] and 37 cardinals 5.53 ± 1.36 days (two-tailed test with unequal variances, $t = 1.833$, df = 76, $0.10 > P > 0.05$) after nest failures (Fig. 1). Variability of the interval length for cardinals was significantly greater than that of catbirds ($F = 2.195$, $P < 0.01$).

Renesting intervals for cardinals were longest and most variable in April and May, and, like catbirds, were shortest in early June and later increased slightly (Fig. 1).

We divided the 25 intervals recorded for cardinals before 17 May, when interval length was the most variable (Fig. 1), into two groups: (1) those associated with below average temperatures on the day of nest failure and on the next 2 days (i.e., the days when a female usually begins to rebuild and when oocytes for the next clutch could begin rapid yolk deposition) and (2) those associated with above average temperatures on those days. Only 3 of the cold weather renestings (N = 11), but 12 of the other renestings (N = 14) occurred within 6 days (G-test with Yates' correction, $G = 6.752$, df = 1, $P < 0.01$).

TABLE 1

FREQUENCY OF DIFFERENT INTERVALS BETWEEN NEST FAILURE AND THE FIRST REPLACEMENT EGG RELATED TO NESTING STAGE WHEN NEST FAILED

Nesting stage and species	Interval (days)										
	3–4[a]	4	4–5	5	5–6	6	6–7	7	7–8	8	9
Laying											
Catbird				3	2	2		1	1		
Cardinal[b]				3		1		1			
Incubating											
Catbird	2	5	2	10		3	1				
Cardinal		8		14	1	7	1	2		3	
Brooding											
Catbird	1	1	2	2	1	2					
Cardinal		1		9		2				1	1

[a] Indicates that interval could have been 1 of 2 days (e.g., 3–4 indicates interval of 3 or 4 days).
[b] Only cardinal nests that failed between 17 May and 15 August were used to exclude extreme variability of intervals in April and May.

Interval lengths following loss during incubating or brooding by catbirds did not differ significantly (Wilcoxon two-sample test, $t = 0.266$, $P > 0.5$). Intervals were longer following loss during the laying stage (laying vs incubating, Wilcoxon two-sample test, $t = 2.399$, $P < 0.02$; laying vs brooding, Mann-Whitney U-test, $U = 62$, $0.10 > P > 0.05$) (Table 1). The length of intervals for cardinals was not significantly affected by the stage at nest failure (Kruskal-Wallis test, adjusted $H = 0.3677$, df = 2, $P > 0.8$).

Discussion.—Our observations agree with those of Mousley (1917) and Chance (1940) who reported that many species of north-temperate-zone passerines relay within 5 to 7 days of nest failure.

The retarding effect of cold weather on reproductive activity, noted in female cardinals, is known for other species (e.g., Nolan 1978:185) and causes much variability in nesting activity early in the breeding season. Finch (1984), who studied another species with a long nesting season, also noted that the greatest range in length of renesting intervals occurred early in the season, as in cardinals.

Catbirds had a marginally shorter renesting interval than did cardinals. The difference, although significant only at $P = 0.10$, suggests that shorter intervals may distinguish species with short nesting seasons from those with long nesting seasons. The noted difference and the significant difference in variances, however, may simply have resulted from biased sampling, as our data on catbirds were collected in summers from which we have no cardinal data.

The stage at which nest failure occurs may influence the length of the subsequent interval before renesting. The relationship, however, is by no means clear. We found no effect in cardinals, but in catbirds the interval was slightly longer following nest failure during laying. Nolan (1978:117) concluded that the interval shown by Prairie Warblers (*Dendroica discolor*) did not vary upon the nesting stage at loss. For other species, however, Delius (1965) and Anderson (1979) noted that the nesting stage at loss influenced the length of the renesting interval.

TABLE 2

DIAMETERS (MM) OF LARGEST OOCYTES AND WEIGHTS (MG) OF OVIDUCTS RELATED TO THE NESTING STAGE OF GRAY CATBIRDS

Egg in oviduct	Eggs laid	Range of diameters of largest oocytes	Range of weights of oviducts	Nesting stage
Penultimate[a] (N = 3)	2, 2, 2	8.80–10.55 1.85[b]–2.25[b]	—	Laying
Last[a] (N = 2)	3, 4	1.80–2.30	1310–1890	Laying
None (N = 3)	3, 4, 4	2.00–2.60	390–445	Incubation (day 2 or 3)[c]
None (N = 4)	3, 4, 4, 4	2.10–2.25	210–290	Incubation (day 4 or 5)[c]
None (N = 2)	—	2.30–2.45	—	Incubation (day 12)[c]

[a] Judged from size of largest oocyte.
[b] Second largest oocyte.
[c] Inferred from known nesting history of birds.

When a small passerine has completed laying, she will typically have only small oocytes (Payne 1969) (Table 2). Such oocytes can attain maximum size within 4 days (e.g., Krementz and Ankney 1986). The *minimum* possible interval, measured from the day when a nest was last active, preceding the day of the first replacement egg is 5 days (4 days of rapid yolk deposition plus one day in the oviduct). However, as we calculated the interval beginning probably well after nest failure, the 4-day interval in cardinals and catbirds is the minimum possible interval. Some 5-day intervals may also be the minimum possible. Nest failure may occur too late in the day for the largest oocyte to complete its growth in time to be laid after a 4-day interval. Clearly, most catbirds and cardinals cannot renest faster than they do from late May onwards.

The oviduct of a catbird does not reach minimum breeding weight, following laying, until midincubation (Table 2). Thus, if a nest were lost early in the nesting cycle, little renewed growth of the oviduct would be necessary, and this would aid rapid relaying.

When nest loss occurs during early laying, intervals may be 3 days, as in cardinals, or even shorter in other species (Delius 1965, Leinonen 1973). What is the fate of the oviducal egg or the large yolky oocytes that would normally have completed the clutch? Three answers seem possible, other than that of laying the oviducal egg on the ground. (1) The oviducal egg present at the time of nest loss might be retained for several days. This is unlikely as it would be maladaptive. (2) Large yolky oocytes present at the time of nest loss might become atretic. The reabsorption of nutrients might accelerate, exceptionally, the growth of a small oocyte as Barry's data (1962) suggest. (3) The largest mature oocyte might be retained, without growth or atresia, for a few days beyond its expected day of ovulation (see Gilbert and Wood-Gush 1971) and, thus, could be used to initiate the replacement clutch. That is, what might have been the last egg of one clutch becomes the first egg of the next clutch.

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Influence of nest-box placement and density on abundance and productivity of American Kestrels in central Missouri.—When extra nest sites are provided by man, an increase in raptor breeding densities often follows (Newton 1976, 1979). The scarcity of suitable cavities probably limits nesting populations of American Kestrels (*Falco sparverius*) (Cade 1982).

Nagy (1963) erected 9 nest boxes on his 130-ha farm in Pennsylvania, and, during a favorable prey year, 6 pairs of kestrels nested in boxes as close as 34 m apart. In Wisconsin, Hamerstrom et al. (1973) placed 50 nest boxes on a 20,243-ha study area where only 3 nests had been reported during the preceding 20 years; in 5 years kestrels nested 77 times. Craig and Trost (1979) erected 20 nest boxes in Idaho and reported a 30% increase in the number of kestrel nests found during the next 2 years. In British Columbia 24 of 137 nest boxes erected for Barrow's Goldeneye (*Bucephala islandica*) were occupied by kestrels (Savard 1982). Over a 3-year period in Colorado, Stahlecker and Griese (1979) increased the local breeding population of kestrels from 6 to 25 pairs after erecting 25 nest boxes. Between 1977 and 1980 Bloom and Hawks (1983) had kestrels in 31% of 247 available nest boxes in California. Similarly, Wilmers (1983) reported kestrels in 31% of 151 nest boxes during a 2-year study in Pennsylvania and West Virginia.

The objectives of the present study were (1) to determine how placement and density of boxes influence kestrel nesting density and nest-site fidelity, and (2) to compare productivity of kestrels using nest boxes with those using natural nest sites.

Study area.—A 194-km^2 area in Boone County, Missouri, was subdivided into (1) a 90-km^2 control area of farmland interspersed with woodlots, old fields, and meadows, and no nest boxes; (2) a similar 78-km^2 experimental area in which 30 nest boxes were placed in the first year and an additional 20 were placed in the second year; and (3) the city of Columbia, Missouri, and immediate suburbs, which consisted of 26 km^2 with no nest boxes.

Materials and methods.—Kestrels were captured with bal-chatri traps and marked with painted U.S. Fish and Wildlife Service bands and colored plastic jesses. We used a 30× spotting scope and 9× binoculars to observe kestrels for more than 1700 h from September 1981 through August 1984.

Population densities of kestrels were determined by driving a route approximately 120 km long at an average speed of 48 km/h. A lateral distance of 400–1600 m (depending on the physiography) on both sides of the route was covered by 1 or 2 observers. Because the areas were intersected at 1.6 km intervals by a network of highways, streets, and gravel roads, the route allowed complete surveillance of the entire study area. Each survey took about 3 h to complete and included stops at designated spots to obtain counts from areas difficult to observe. At least one survey was completed per week throughout the year during the 3 years of the study.

The possibility of counting the same bird twice was minimized by the number of color-marked kestrels (70 adults) and by keeping track of all birds flying out of an area being surveyed and into an area yet to be covered. Surveys were conducted between 10:00 and 14:00 h on days with conditions of good visibility and low wind velocity. Because of the area's open habitat and kestrel use of powerlines, power poles, snags, and fence posts as perches, we feel our surveys were thorough.

Wooden nest boxes had floors of 25–30.5 cm^2, were 38 cm deep, and had an entrance hole of 7.6 cm diameter near the top. Boxes were placed between 5 and 14 m above the ground. Nest-box sites included buildings, silos, utility poles, and live trees. Nests were visited briefly near the end of incubation to determine clutch size, and again before fledging to count and band the young.

The study area's 232 natural cavities with an estimated diameter of 6–10 cm were measured for depth and width, and subsequently monitored.

Nesting phenology.—There was no difference in date of nest initiation in natural cavities and nest boxes. In 1982, the mean laying, hatching, and fledging dates were 1 April, 6 May, and 6 June, respectively. Hatching and fledging averaged one week later in 1983, when the first nest was initiated more than 1 week earlier, and the latest nest nearly a month later than in 1982. Nesting was 2 weeks later in 1984 than in 1983. The time from earliest to latest initial nestings was just over 30 days during the first year, more than 75 days in the

TABLE 1

NESTING DENSITIES OF AMERICAN KESTRELS IN CENTRAL MISSOURI, 1982–84

Study area	km²	1977–1981[a]		1982		1983		1984	
Urban control	26	5	0.13	6	0.23	8	0.31	6	0.23
Rural control	90	2	0.02	4	0.04	5	0.06	3	0.03
Rural experimental[b]	78	4	0.05	12	0.15	26	0.33	25	0.32
Total	194	11	0.06	22	0.11	39	0.20	34	0.18

[a] No nest boxes during this period.
[b] Control areas had no nest boxes; the experimental area had 30 nest boxes in 1982, 50 in 1983, and 45 in 1984.

second, and about 45 days in the third. In 1983 the unusually warm spring-like weather during winter, coupled with winter weather during early spring, probably caused the prolonged nesting period (Roest 1957). In 1984 an exceptionally wet spring probably caused kestrels to begin nesting 15 days later. Kestrels began copulating and mutual perching in December or January each year. During March and April 1983, when mild weather was regularly interrupted by cold weather, kestrels stopped courting.

Population densities.—Prior to the erection of nest boxes, mean nesting density of kestrels was ca 0.06 pair per km² (1977–81) (Table 1). The number of nesting kestrels increased markedly in the area after the 50 nest boxes were in place in 1982 and 1983 (Table 1). Kestrels nested in 53% of the 125 boxes available during the 3 years of the study.

The notable increase in nesting kestrels between 1982 and 1983 may be due to the simultaneous increase in food abundance and nest availability, while the slight decline from 1983 to 1984 may be the result of a marked decrease in food supply. Although we did not quantify population densities of rodents, observations and interviews with farmers throughout our study area indicated a high vole (*Microtus* spp.) population in 1983 and a crash in 1984.

In the experimental area, densities of wintering kestrels increased from 0.22 birds/km² during winters preceding the study to 0.30 birds/km² during the first year (1982), 0.40 birds/km² during the second year, and 0.42 birds/km² during the third year of the study. The difference between the years preceding and following erection of the boxes was significant ($\chi^2 = 5.34$, df = 1, $P < 0.05$). During the winter of 1982–83 kestrels roosted in all 50 boxes. Mills (1975) mentioned the importance of winter roost availability as a factor limiting kestrel populations in Ohio. We also saw kestrels using the tops of nest boxes as feeding platforms during winter, and during several sleet storms kestrels hunted while perching in the nest-box hole.

Location of natural nests and nest-box sites.—Natural nest sites used by kestrels in the study area included buildings (84%), both abandoned and occupied, and cavities made by Northern Flickers (*Colaptes auratus*), Pileated Woodpeckers (*Dryocopus pileatus*) and Red-headed Woodpeckers (*Melanerpes erythrocephalus*) (16%). Two of the woodpecker cavities used by kestrels were in trees or snags; 3 were in power poles.

Kestrels seemed to prefer to nest in nest boxes even when there was an abundance of suitable natural cavities nearby (see also Hamerstrom et. al 1973). Nest boxes that were placed within 20 m of woodlots, however, were used by fox squirrels (*Sciurus niger*), which sometimes evicted kestrels. Wilmers (1983) reported that kestrels avoided nest boxes near the borders of woods.

Kestrels rarely used boxes on live trees, using both poles ($\chi^2 = 52.10$, df = 1, $P < 0.01$)

TABLE 2
NEST-BOX USE BY BREEDING AMERICAN KESTRELS IN BOONE COUNTY, MISSOURI, 1982–84

Nest-box location	No. available	% of available used	% nesting success[a]
Utility poles	61	79	78
Building and silos	22	68	64
Live trees	42	7	33
All sites	125	53	73

[a] A successful nest was one that fledged young.

and buildings ($\chi^2 = 28.05$, df = 1, $P < 0.01$) significantly more often. Stahlecker and Griese (1979), working in Colorado, also reported a high occupancy rate (73%) in boxes on power poles.

Nesting success.—In 14 instances nest boxes were used by kestrels but no eggs were laid. Eggs were laid but nests failed in 8 cases, 3 of these clutches were destroyed by raccoons, 3 had broken eggs, and at 2 sites the eggs failed to hatch.

Young fledged from 52 broods in 46 boxes involving 43 pairs (including second broods) (Toland 1985). Thus, at least one young fledged from 70% (46 of 66) of the boxes used. Nesting success (total young fledged divided by total eggs laid) of kestrels in pole-mounted and building-mounted boxes was 78% and 64%, respectively (excluding a box where a yearling pair hatched 1 of 13 eggs laid). Pairs nesting in boxes on trees had a nesting success of 33% (Table 2). The nest success rate in pole-mounted boxes was significantly higher than in boxes on trees ($\chi^2 = 11.76$, df = 1, $P < 0.01$), but the difference between building-mounted boxes and tree-mounted boxes was not statistically significant ($\chi^2 = 3.78$, df = 1, $P > 0.05$).

Physical characteristics of natural and nest-box sites were similar. The average height of nest boxes was 7.2 m; that of natural sites averaged 9.8 m ($\chi^2 = 0.40$, df = 1, $P > 0.05$). Kestrels used 72% of the 7-m or higher nest boxes, but only 36% of the 6-m or lower boxes ($\chi^2 = 11.60$, df = 1, $P < 0.01$). The average diameter of the nest hole was 7.6 cm in nest boxes and 9.4 cm in natural cavities ($\chi^2 = 0.20$, df = 1, $P > 0.05$). The average distance from the nest to the favorite plucking post was 20.5 m from boxes and 30.0 m from natural sites ($\chi^2 = 2.0$, df = 1, $P > 0.05$). Kestrels nesting in natural sites seemed to prefer southerly or easterly openings (68%), even though there may have been more available cavities facing north or west because buildings in the area deteriorate more severely from weathering on their north and west sides. Kestrels chose nest boxes with southerly or easterly openings 67% of the time. Other studies describe similar south and east orientations (Balgooyen 1976, McComb and Noble 1981, Brauning 1983), as well as a preference for higher nest cavities (Brauning 1983). The former most likely protects birds from northerly storms and increases solar exposure, while the latter increases protection from ground predators (Balgooyen 1976, Brauning 1983).

Annual productivity.—During the first year, hatching success in boxes was less than half that found in natural cavities (Table 3). This is in part attributable to predation by raccoons (3 clutches) and other disturbances (4 clutches cracked). Although care was taken to simulate natural nest sites when placing nest boxes, some sites may have been more accessible to predators. After moving 3 tree boxes that suffered predation in 1982 to new sites less accessible to mammalian predators, no predation occurred in these boxes during the following 2 years. The sudden availability of nest sites after placement of the boxes may have allowed inexperienced yearlings and adult nonbreeders to nest (Newton 1976, 1979). Two

TABLE 3

SUCCESS OF AMERICAN KESTREL NESTS IN BOXES VERSUS THOSE IN NATURAL CAVITIES IN BOONE COUNTY, MISSOURI, 1982–84

Site	No. pairs	Total no. eggs	No. nesting attempts	% hatching success	No. fledged	% fledging success[b]	Productivity[c]	% overall nesting success
Nest boxes								
1982	6	44 (4.8)[a]	15	34	15	100	2.5	34.1
1983	23	172 (5.3)	124	72	123	98	5.4	71.5
1984	17	81 (4.8)	72	89	69	96	4.06	85.2
All years	46	297 (5.0)	211	71	207	98	4.5	70.0
Natural cavities[d]								
1982	11	63 (5.0)	57	90	54	95	5.0	85.7
1983	13	80 (5.2)	71	89	71	100	5.46	88.8
1984	4	19 (4.8)	15	79	14	93	3.5	73.7
All years	28	162 (5.1)	143	88	139	97	5.0	86.0

[a] Mean size of initial clutches shown in parentheses.
[b] Number fledged divided by number hatched.
[c] No. fledglings/nest.
[d] Includes woodpecker cavities and holes in buildings.

kestrels produced in boxes in 1982 subsequently nested as yearlings in boxes in 1983. One was a yearling female paired with a color-marked male yearling that produced one fledgling from 13 eggs. The other was a color-marked yearling male mated with an adult female where 5 eggs were infertile.

Reuse of nest-sites.—Successive use of the same territory for at least 2 years occurred in 70% of the color-marked nesting pairs. Consecutive use of the same nest sites occurred in 62% of these pairs.

Six boxes used in 1982 were reoccupied in 1983, and 18 boxes used in 1983 were reused in 1984. One nesting site on a building was occupied for at least 6 successive years (J. Peters, pers. comm.), and another was used for at least 5 years. A natural cavity was occupied by kestrels during 4 consecutive years, and 4 other cavities were used for at least 3 years each. Craighead and Craighead (1956) reported a kestrel pair using the same nest for 6 consecutive years, and Balgooyen (1976) reported that 61% of the nesting territories he studied were reoccupied.

Summary.—Both nesting and wintering populations of kestrels increased significantly after implementation of nest boxes. More "natural" nests were in buildings than in tree cavities. Similarly, kestrels nested in nest boxes mounted on buildings and utility poles significantly more often than they nested in tree-mounted nest boxes. Nesting success was significantly higher in boxes mounted on man-made structures than on trees. Physical characteristics of nest sites, including nest height, orientation, cavity-hole diameter, and distance from plucking perch, were similar for boxes and natural cavities. Although nesting success of kestrels using nest boxes was lower than in natural nest sites during the first 2 years of the study, the persistent nature of nesting kestrels (double broods, replacement clutches) enabled them to produce the same number of young per nest in nest boxes as in natural sites.

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Close inbreeding in the Merlin (*Falco columbarius*).—Inbreeding in natural populations of birds has been reported for only a few species (Shields 1982, Koenig et al. 1984, Woolfenden and Fitzpatrick 1984, Millington and Price 1985, Rowley et al. 1986). We report here the first recorded instance of close inbreeding in a falconiform, the Merlin (*Falco columbarius*).

The inbreeding Merlins, a mother-son pair, were discovered in June 1986, as part of a study of an urban population of Merlins in Saskatoon, Saskatchewan, Canada (Oliphant and Haug 1985). Both members of the pair had been banded as chicks, the mother in 1982 and her son in 1984. Thus, their respective ages when breeding together were four and two years. The female had moved 1.9 km from her 1985 nest site where she had bred with a different male. Her son had not been captured before. Breeding pairs in this population occasionally have yearling helpers (James and Oliphant 1986); however, no other Merlins were seen in the vicinity of the nest, and we believe these two birds were the only ones present. To date, 11 other breeding pairs have been trapped where both partners had been banded as chicks. None of these pairs involved closely related birds. Newton (1986) found no cases of inbreeding in a much larger sample of European Sparrowhawks (*Accipiter nisus*).

The mother-son pair fledged five chicks. The average number of young produced by successful nestings (N = 68) in our population is 4.2 chicks (Oliphant and Haug 1985). Therefore, there was no evidence of the inbreeding depression that has been reported in other species (Greenwood et al. 1978, but see Shields 1982 and Rowley et al. 1986).

Female Merlins in this population show a greater mean natal dispersal (24.2 ± 64.6 km [SD], N = 15) than do males (4.0 ± 3.1 km, N = 21) (cf. Greenwood and Harvey 1982). The dispersal distance of the mother was 2.1 km, and that of her son 1.9 km, both less than the average. In a larger sample of inbreeding Great Tits (*Parus major*), Greenwood et al. (1978) established that the inbreeding males had dispersed more than the average, and the inbreeding females less than the average.

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Rediscovery of the Rufous-crested Coquette (*Lophornis delattrei brachylopha*) in Guerrero, Mexico.—The occurrence of the Rufous-crested Coquette (*Lophornis delattrei*) in Mexico has been questioned ever since Moore (1949) described a new race of the species based on two males collected in San Vicente de Benitez, Guerrero, by Chester C. Lamb in May 1947 (type specimen in Moore Collection, Occidental College, Los Angeles, California).

Because it is otherwise unknown north of central Costa Rica (four specimens from the San Jose region), where it is at best a vagrant (AOU 1983), the Rufous-crested Coquette is believed to be "accidental (?)" (Peterson and Chalif 1973) in Mexico. The species occurs regularly from western Panama (Veraguas) to the Magdalena valley of Colombia and in eastern Peru and east-central Bolivia (Friedmann 1950, Blake 1953, Wetmore 1972, Ridgely 1976, AOU 1983). The AOU Check-list (1983) omits all mention of Mexico in the distribution of *L. delattrei.* Here I report the rediscovery of this species in Guerrero, Mexico, based on the collection of three specimens. These specimens indicate that the species is resident, and they validate Moore's (1949) description of the race *brachylopha.*

In the course of field work in Guerrero in 1986, expeditions of the Ornithological Collection (COIBUNAM) collected 3 specimens of *L. delattrei,* one male and two females, at Arroyo Grande, 13 km NE of Paraiso, on 23 January, 29 April, and 1 May. All specimens were collected in mist nets in evergreen subtropical forest at an elevation of 1350 m (see vegetation in Miranda and Hernández 1963). The two specimens collected April and May were molting and had much breast fat and undeveloped gonads.

At the same locality, the following species of hummingbirds also were present: Long-tailed Hermit (*Phaethornis superciliosus*), White-eared Hummingbird (*Hylocharis leucotis*), Berylline Hummingbird (*Amazilia beryllina*), White-tailed Hummingbird (*Eupherusa poliocerca*), Amethyst-throated Hummingbird (*Lampornis amethystinus*), Long-billed Starthroat (*Heliomaster longirostris*), Sparkling-tailed Hummingbird (*Tilmatura dupontii*), Bumblebee Hummingbird (*Atthis heloisa*), and Rufous Hummingbird (*Selasphorus rufus*). This is the only locality in Mexico that *L. delattrei* has been recorded, except for the type locality.

The male specimen has the same characteristics described by Moore (crest much shorter, about half as long, with no spangles on the tips of the feathers) (Table 1). Hardy and Webber (1975) compared the only two known specimens of *L. d. brachylopha* and agreed with Moore's description, except that "the alleged shorter crest of *brachylopha* is entirely a result of wear . . . ." Female specimens differ from previous descriptions in the literature (Blake

TABLE 1

MEASUREMENTS OF *LESSONI* AND *BRACHYLOPHA* SUBSPECIES (MM)

	Wing	Tail	Culmen[a]	Crest[b]
lessoni from Panama and Colombia (Wetmore 1972)				
♂ (N = 12)	38.1 (37.1–40.2)[c]	21.6 (20.0–22.9)	11.4 (10.7–12.8)	20.3 (17.9–21.5)
♀ (N = 6)	36.9 (35.8–37.9)	18.9 (18.0–20.2)	11.8 (10.7–12.7)	
brachylopha from Guerrero, Mexico (Moore and the author)				
♂ (N = 3)	41.0 (39.9–41.9)	24.6 (23.8–25.4)	12.7[d]	11.1 (10.5–11.7)
♀ (N = 2)	43.8 (42.4–45.2)	23.8 (22.7–25.0)	12.9 (12.8–13.0)[d]	

[a] Measured from base to the tip.
[b] The length of the crest was measured from the base of the anterior long crest feathers to the tips of the longest one.
[c] Mean (range).
[d] Measured differently from Wetmore (1972).

1953, Peterson and Chalif 1973) in throat coloration. A better description could be "lacks crest, but crown rufous, throat completely white, lateral rectrices rufous-tipped, and with a broad black subterminal band, belly grayish brown, and crissum cinnamon." The three specimens agree with Moore's description of *brachylopha* and show that both males and females differ noticeably from those of *lessoni,* the nearest race (Table 1).

Other species (e.g., *Ornithion semiflavum, Rhodinocichla rosea, Sporophila schistacea*) have similar discontinuous distributions, with populations in Mexico and Costa Rica or Panama (Slud 1964, Wetmore 1972). Such distributions may be a result of the isolation of southern Mexico as a forest refuge during the last Pleistocene interglacial period (F. G. Stiles, pers. comm.).

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Abnormally colored juvenile Black-capped Chickadee molts to normal basic plumage.— On 29 July 1986, at Aberdeen, Brown County, South Dakota, I netted, banded, and photographed (VIREO accession numbers V06-2-003, V06-2-004) an aberrantly plumaged Black-capped Chickadee (*Parus atricapillus*). In general appearance, the bird was brown where normal birds are gray, a condition known as "leucism" (see discussion in Campbell and Lack, eds., A dictionary of birds. Buteo Books, Vermillion, South Dakota, 1985). The bird resembled a Boreal Chickadee (*P. hudsonicus*), but its throat was not black and its back was pale mouse-brown, characteristics that are typical of "leucistic" plumage. Close examination of the crown and throat, which were chestnut, revealed a few scattered black feathers molting into the plumage. The underparts were white except for some buff just below the bend of the wing (similar to that found in Black-capped Chickadees). The lower flanks were white. The remiges and rectrices were pale mouse-brown with white edges; the bases of these feathers were gray (the gray area was longest on the tail, comprising 37 mm of the 64 mm tail; and on the primaries, where 34 mm of the 68 mm were brown). The lesser secondary coverts were gray. The cheeks were completely white. The eyes and other softparts were typical for Black-capped Chickadees. The bird's skull was incompletely ossified, indicating a first-year bird. The bird appeared to be in the company of several normally plumaged Black-capped Chickadees that I banded during that week.

The bird was subsequently trapped and released 5 times. On 24 August 1986, the bird was well into prebasic molt. At this time, the crown and throat were largely black, with only a broad chestnut superciliary stripe and postocular region. The brown stripes nearly, but not quite, met at the back of the crown. Scattered brown feathers remained at the edges of the black throat. The bird's flanks were buffy. The back was a normal gray, as were all the secondary coverts (although the alula, primary coverts, and tail were as before). The flight feathers remained unmolted, except for the secondary nearest the body on each side, which were now normally colored. No remiges or rectrices appeared to be missing. On 14 September, all that remained of the chestnut on the head were postocular spots and a few preocular feathers. On the right wing, a gray second secondary to the body was appearing. The corresponding secondary on the left side was still brown and seemed exceptionally worn; otherwise the bird was similar to its August appearance. On 8 October, the 3 inner right secondaries and the innermost left secondary had been molted and were normally colored. By 18 January 1987, the wing molt situation had not changed. The left third and forth secondary to the body were now becoming excessively worn, as were the 2 left outer tail feathers. The third to the outside left rectrix, however, was a newly molted and normally colored feather.

The first basic plumage in the Black-capped Chickadee is acquired by a partial prebasic molt, which involves the body plumage and wing coverts, but not the rest of the wings or tail (Dwight, The sequence of plumages and moults of the passerine birds of New York. N.Y. Acad. Sci. 13:73–360, 1900). This chickadee's molting of a few flight feathers at an uncharacteristic time may be due to geographical irregularity in molt pattern or replacement of individual lost feathers.

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A circular "ring-angel" movement by field-feeding waterfowl.—The pattern of dispersal of birds from communal roosts has been termed "ring-angel" because of the images that the flocks produce on radar screens (Harper 1959, Eastwood et al. 1962). This pattern of movement from roosts has been discussed in relation to central place foraging and food competition avoidance (cf. Hamilton and Watt 1970), but it has not been examined in terms of flock movements of feeding birds. In this paper, we describe a "ring-angel" distribution, along with the movements and amounts of grain eaten by feeding Mallards (*Anas platyrhynchos*) and Greater White-fronted Geese (*Anser albifrons*) near Last Mountain Lake, Saskatchewan.

Observations.—The events reported here occurred between 17:20 and 20:00 h on 22 September 1982 in a 125-ha harvested barley field (six-row variety). Observations of feeding Mallards and geese were made with binoculars and a spotting scope from 4 m up in a tree at distances of from 50 to 200 m from the flock. The birds' landing locations and subsequent movements could be determined accurately. Thirty-four Greater White-fronted Geese had been feeding in the field for 20 to 30 min before most Mallards began arriving at 18:00 h. As flocks of Mallards arrived they landed centrally within the flock rather than at its edges. They then gradually dispersed outward from these central positions, producing a very clear, circular "ring-angel" pattern (cf. Harper 1959, Eastwood et al. 1962). During the next hour, Mallards, and smaller numbers of geese and Northern Pintails (*Anas acuta*), continued to land inside the ring-angel and then walked outward to join feeding birds. Approximately 5600 ducks and 300 gecse were involved in the ring-angel which was estimated to be about 200 m in diameter when they left the field.

It was not possible to observe feeding birds the next morning (23 Sept.) because of hunting in the field. However, we sampled several parts of the field, including where ducks and geese had fed the previous evening and adjacent areas that had not been used. A 0.29-m^2 hoop was tossed >5 m ahead as we walked through these areas. The ground was searched for feathers and droppings to ensure that the proper areas were sampled. The number of grain heads, number of plant stems, and height of the stem nearest the center of the hoop were recorded for each toss. The number of heads/toss was then assigned to one of the following categories: 0, 1, 2, 3, >3. The number of kernels inside the hoop was estimated and was categorized as follows: <5, 5–15, 16–50, and >50.

Results and discussion.—The amount of grain missed by harvest machinery (waste grain) and plant (stubble) characteristics in the two areas differed. First, the average number of grain heads/toss was significantly lower inside the ring-angel (1.3 ± 1.7 [SD], N = 36 hoop tosses) than outside (5.3 ± 10.9, N = 67) (G-test, $P < 0.01$), and there were fewer loose kernels inside the ring-angel than outside (G-test, $P < 0.05$). Waterfowl ate about 75% of the barley. In lure crop studies (R. G. Clark and H. Greenwood, unpubl. data), we found that ducks "gave up" feeding in swaths (windrows) of cut grain when 75–80% of the grain

was eaten, possibly because it then became too difficult to find the remaining grain. These results concur with Baldassarre and Bolen's (1984) report that ducks removed about 80% of waste corn from fields in Texas during winter. Second, plants were less dense (t-test, $P < 0.05$) inside the ring-angel area ($\bar{x} = 27.3 \pm 15.1$, N = 36) than outside ($\bar{x} = 44.7 \pm 17.4$, N = 67), but plant height was similar inside ($\bar{x} = 12.5 \pm 5.5$, N = 36) and outside ($\bar{x} = 14.6 \pm 3.8$, N = 67) the ring-angel (t-test, $P > 0.05$). Bossenmaier and Marshall (1958) proposed that waterfowl prefer areas with low plant density and short height because it is easier for them to land, but as far as we know this is the first evidence to support this idea.

Ring-angels never developed when we observed waterfowl feeding in lure crops, where grain was concentrated in swaths (windrows), or in harvested fields where waste grain was concentrated where the swath had been picked up by a combine. In those fields, ducks and geese lined up along the swaths, where feeding appeared to be most profitable. For instance, in 1984, waste grain density along the path of the combine (a band about 1-m wide) averaged 69.2 ± 54.0 g/m^2 (N = 24 barley fields), whereas density in the area between these bands (about 5 m wide) averaged only 2.3 ± 1.9 g/m^2. In contrast, average waste grain density was 23 ± 48 g/m^2 in the ring-angel field, assuming that heads of barley contained an average of 1.25 g of kernels (Clark et al. 1986), and we found no evidence of harvested swaths (i.e., waste grain was relatively dispersed).

We suggest that as grain was eaten inside the ring-angel, the "biodeterioration zone" (Hamilton and Watt 1970:265) increased in size, forcing birds to move outward in search of more abundant food. The ring-angel formation enabled many birds to scan all directions simultaneously, possibly improving predator detection. We have no idea how often the ring-angel formation occurs and, unfortunately, as most waterfowl feeding behavior is recorded at ground level, the pattern, if present, would usually be missed. Further work is needed to ascertain the conditions favoring the development of this feeding pattern (e.g., Sih 1980).

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Boat-tailed Grackle lays eggs in abandoned nest containing eggs.—On 6 May 1986 in a cattail (*Typha angustifolia*) marsh at Magnolia Gardens, Charleston County, South Carolina, I found a Boat-tailed Grackle (*Quiscalus major*) nest that had 6 eggs. My data for this nest are 19 April, 3 eggs; 28 April, 3 eggs; 6 May, 6 eggs; 17 May, nest empty, but not disheveled, nor with any eggshell fragments. On 17 May a Yellow Rat Snake (*Elaphe obsoletus*) was resting in another Boat-tailed Grackle nest 1.5 m from the subject nest, and it is possible that the snake had taken the contents of both.

During 1983–1986 the mean clutch size of 489 Boat-tailed Grackle nests that I followed was 2.77 ± 0.51 [SD]. The frequency distribution of clutch sizes is repulsed (i.e., there are more observations than expected at the center of the distribution, and fewer at the tails) (Sokal and Rohlf, Biometry, Freeman, San Francisco, California 1969). As suggested by Yom Tov (Biol. Rev. 55:93–108, 1980), in species with such frequency distributions, if any clutch is more than twice the size of the mean, it is reasonable to assume that it was laid by more than one bird. In this population I have found only 6 4-egg clutches (0.8% of sample), and I have not found any 5-egg clutches.

Although the history of the nest is incomplete, I believe the following happened: A bird laid three eggs, and then either abandoned the nest or was incapacitated. I infer this because the incubation period for Boat-tailed Grackles in this population is 13.5 days and the interval between my last visit to the 3-egg nest and the deposition of the additional three eggs was 18 days. About the same time that the nest was abandoned, another female lost her nest just after its completion, and found an available, undefended nest in which to deposit her eggs. The six eggs were incubated by the second female, as they were warm when I examined them on 6 May. Another possibility is that a single female laid 2 clutches in the same nest.

In the cattail colonies that I studied, nest sites were limited, as the grackles used dead vegetation that had stood through the winter. I have found no other instances of nest reuse, however. The behavior reported here therefore appears to have resulted from an unusual combination of circumstances. It cannot be classified as brood parasitism, as the nest and eggs of the first female had probably been abandoned. The interesting aspect is that if a second female was involved, she did not remove the previous eggs before depositing her own.

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ORNITHOLOGICAL LITERATURE

THE BREEDING BIRD SURVEY: ITS FIRST FIFTEEN YEARS, 1965–1979. By C. S. Robbins, D. Bystrak, and P. H. Geissler. U.S. Fish and Wildlife Service, Resource Publication 157, Washington, D.C., 1986:196 pp., 77 numbered figures (including 27 maps and 366 graphs), 5 tables, and 8 appendices. No price given (paper). (Order from Publications Unit, U.S. Fish and Wildlife Service, Washington, D.C. 20240.)—Collectively, the authors have already contributed some 20 publications relating to the Breeding Bird Survey (BBS) and uses of its data, and are to be commended for their continuing efforts on behalf of this program. Almost certainly, the present work is intended as a broad overview that (1) condenses a large portion of the voluminous BBS data file, (2) advertises the BBS as a source of baseline data for population and other studies, (3) encourages interest and participation in the BBS, and (4) acknowledges the assistance of thousands of volunteers, without whom the BBS could not have progressed so far. For some readers, the authors' success in meeting these objectives will be overshadowed by their failure to satisfactorily "discuss the more important population trends detected by the survey in its first 15 years."

After a lengthy abstract, the book begins with short sections on "Field Procedures," "Data Processing and Analysis," "Bias Evaluation," and "Improvements in Editing and Analysis Techniques." The body of the work is a species by species account of observed regional trends gleaned from 12 to 15 years of BBS data. Information for over 240 species, recognizable subspecies, and groups of related species is presented, in most cases both textually and graphically. Following these accounts are brief sections on "Mapping of Relative Abundance," "Other Uses of BBS Data," and "Conclusions." Tables list the total number of individuals of all species and the number of routes on which they were found in 1977; the mean number of birds of a given species detected per route in all states and provinces from 1965 to 1979, and the total number of routes, total species, individuals per route, and species diversity index (H′) for each of 62 physiographic regions sampled by the BBS. Appendix F provides an index to published maps of the relative abundance of 240 species based on BBS and Christmas Bird Count data.

Although superficially thorough and admirable in scope, the publication is disappointing and frustrating in a number of respects:

(1) The work is inconsistent with respect to avian nomenclature and taxonomic order. Species in the text, and those listed in all but one of the tables and appendices, are named and sequenced according to the fifth edition of "The A.O.U. Check-list of North American Birds" and its 32nd and 33rd supplements. Appendix A ("Common and Scientific Names of Avian Species Mentioned") uses sixth edition scientific nomenclature and English name changes (the latter in brackets), but orders the species according to the fifth edition. It is difficult to dismiss this potentially confusing inconsistency, given that sixth edition nomenclature has been accessible since July 1982 (Auk 99 [supplement]:1CC–16CC).

(2) The authors fracture their data into too many geographic subsets. Species accounts are riddled with trend and other information for the entire continent and for any of three BBS regions, seven geographic subregions, 62 physiographic regions or strata, and 60 states and provinces. The latter division seems unwarranted in light of the authors' comment (p. 14) that "For any species, knowledge of the preferred strata gives more insight into the requirements of the species than does a comparison of relative abundance among States and Provinces." Also, one of the authors (Bystrak; Sialia 1:74–79, 87; 1979) has noted that "Better measurement of change can be obtained by the use of ecological regions than by combining data on a state or province basis . . . ." On the other end of the geographic scale, the authors might well have refrained from continent-wide analyses and concentrated only

on subregional and/or physiographic information. Still frustrating, however, would be the fact that a map on p. 12, showing the boundaries of the 62 physiographic regions referred to by name throughout the text, has these regions identified by number only and must be repeatedly keyed to Table 5 (pp. 158–159) which provides the name of each stratum.

(3) Analyses are attempted for too many species, including those that the BBS arguably, and even admittedly, does not sample well or without substantial bias (e.g., many nonpasserines, species with suboptimal sample sizes, birds that are difficult to identify or easy to misidentify, late nesters, species for which nonbreeding individuals may be more obvious than those breeding, and species for which the roadside populations sampled by the BBS may not be representative of larger populations that nest away from roads). Too often the authors ignore these and other sources of bias and present analyses anyway. On p. 14 we are given trends for native colonial herons, despite the fact that "Colonial nesting herons are not easily monitored by the BBS"; on p. 30, similar information is given for owls and goatsuckers, although "These nocturnal birds are poorly sampled . . . ." Several combined analyses are presented in an attempt to provide information about species with smaller sample sizes (pp. 16, 18, 23, 36, and 92), despite the admission that the more common species in these groups have an "undue influence" or "overriding effect" on the observed trends. For these and other reasons, perhaps a third of the species included in the book should have been omitted.

(4) By choosing a species by species format, the authors have missed several opportunities for interspecific comparison and have made a less meaningful biological and biogeographical contribution than they might have. The few group analyses provided (e.g., for native colonial herons, waterfowl [4 spp.], non-Killdeer shorebirds, western hummingbirds, non-flicker woodpeckers, flycatchers, vireos, and the genera *Vermivora* and *Dendroica*) combine species that are not comparable in many respects. A statement on p. 6 that ". . . analyses are performed for certain key habitats by combining data for several species that are typical of a particular habitat . . . ," finds no support in the body of the work. Nowhere do we find detailed comparative or summary analyses for species with shared breeding or wintering habitats or ranges, or with similar migratory habits; for species apparently displacing or being displaced by other species; or for the several species that the authors suggest exhibit winter-kill effects. While some of this information can be distilled from the work, the authors would have made a better case for the usefulness of their data had they taken this task on themselves.

Although the authors attempt a few direct comparisons between species, not enough was made of one such comparison, and too much was made of another. In the latter case (p. 67), they point to a "*close parallel*" [italics mine] between the eastern trends for the Carolina Wren (*Thryothorus ludovicianus*) and the Gray Catbird (*Dumetella carolinensis*), hinting that the unusually severe winters of 1976 and 1977 affected the species similarly. In what can only be described as an understatement, they qualify this with the remark, ". . . except that the population changes for the Gray Catbird were not nearly so severe, probably because this species winters several hundred kilometers farther south and therefore is not exposed to prolonged, severe cold." In the other case, although I looked forward to a detailed comparison of Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) warblers, the authors wrote simply (p. 92), "Despite reports that the Golden-winged Warbler is losing ground in competition with the Blue-winged Warbler, the Golden-winged Warbler population appears to be stable across the continent." Fortunately, they provide details, which although unintegrated, are more telling. The Golden-wing showed a significant decline only in the Great Lakes subregion and Wisconsin, but Wisconsin is the only state in which Golden-wings were more than twice as numerous as Blue-wings. The Blue-winged Warbler account, just two sentences long, indicates that this species increased in West Virginia, the

state with the highest average count of Golden-winged Warblers. Thus, Golden-winged Warblers seem to be losing ground in areas where they are most numerous; a fact arguably of greater biogeographical interest than the vague notion that the Golden-wing population is stable across the continent.

An undue concern for the continent-wide stability of a species or other taxon is expressed throughout the text. On p. 36 we learn that "Although some species of flycatchers have been decreasing, . . . data show that there is no continent-wide problem affecting the flycatcher family." Details given frequently provide a clearer picture, but such general statements can be misleading and may have an overriding effect on the conclusions drawn by all but the more careful readers and those experienced in bird study.

(5) Many of the causal relationships proposed by the authors between various phenomena and observed population trends for select species, constitute incomplete, speculative, or conflicting explanations that are unsatisfactory or unconvincing. On p. 98, a declining House Sparrow (*Passer domesticus*) population in the East over the past 60 years is attributed in part to the replacement of horses with automobiles, and to a ". . . continuing trend toward cleanliness in dairy barns, and to a lesser extent in other farming operations." But on p. 104, the authors partly account for an increase in Common Grackles (*Quiscalus quiscula*) with ". . . the trend toward mechanical harvesting of crops which leaves *more* [italics mine] waste grain . . . permit[ting] increased winter survival . . . ." In the case of the House Sparrow, might not this, as well as the trend toward more backyard bird feeding, balance the purported trend toward cleaner barns?

The authors point to the severe winters of 1976 and 1977 in their explanations for declines in several species. While these probably do account for coincident sharp drops in the mean annual counts of a number of less hardy species, it is an unlikely explanation (although the authors suggest it on p. 63) for a pronounced downward trend, since 1972, for the Bewick's Wren (*Thryomanes bewickii*) in the Central and Eastern regions. I was surprised, given the considerable speculation since before the turn of the century, to find no discussion of the influence of the House Wren (*Troglodytes aedon*) on eastern Bewick's Wren populations.

Still other analyses seem incomplete. On pp. 53–54, in their analysis of Black-capped Chickadee (*Parus atricapillus*), the authors ". . . found no correlation between the breeding populations anywhere in the Northeast and the years in which autumnal irruptions were detected along the coast of Massachusetts . . . ." But their published analysis, at least, does not include information for Maine, a state that has twice proved to be the origin of fall migrant chickadees captured at Powdermill Nature Reserve, a banding station in the mountains of southwestern Pennsylvania.

Sometimes data given do not support the authors' contentions. Their statements on pp. 1 and 123, respectively, that "Effects of urban and suburban expansion are often reflected in the loss of forest interior birds," and ". . . those species dependent on forest interior habitats . . . are disappearing from many areas," are contradicted by their data, which show that only a few woodland species registered significant declines. On p. 96, the authors point out that "Despite loss of habitat through fragmentation of forests, the Ovenbird [*Seiurus aurocapillus*] has continued to show an increase . . . ." Oddly enough, they implicate habitat loss only in their explanations for declines of species characteristic of early successional or scrub habitats (e.g., Prairie Warbler [*Dendroica discolor*], Yellow-breasted Chat [*Icteria virens*], Field Sparrow [*Spizella pusilla*], and Loggerhead Shrike [*Lanius ludovicianus*]). Those who believe that these species are declining even where such habitats are artificially or naturally maintained (e.g., power line rights-of-way and fire-prone scrub), may not be convinced.

The authors have largely ignored or overlooked factors "south of the border" which might have influenced trends in North American breeding bird populations during the period

considered. In their explanation for only one trend, that of the Scissor-tailed Flycatcher (*Tyrannus forficatus*) (p. 36), do the authors suggest that ". . . for a possible explanation we should perhaps look to southern Mexico and Central America where [the] species winters." On p. 3, they state that it might take another decade's worth of data to ". . . enable the . . . measurement of effects of changing land use on avian populations both here and on the tropical wintering grounds . . . ." Even so, the reader must consider that the apparent population increases of so many species that are woodland nesters, neotropical migrants, or both, may be symptomatic of certain biases inherent in the BBS. In any case, a thoughtful discussion of this surprising result would seem to have been in order.

The above criticisms notwithstanding, the value of long-term studies such as the BBS cannot be overstated. And while probably the best information given (e.g., on relative abundance and species composition and diversity) is the most briefly considered, the present work nonetheless validates the BBS as a productive data source. At the same time, and perhaps inadvertently, it highlights the need for extreme care in the interpretation of these data and the need to know what it is that the BBS most reliably measures.—ROBERT S. MULVIHILL.

HANDBOOK OF THE BIRDS OF EUROPE, THE MIDDLE EAST, AND NORTH AFRICA. THE BIRDS OF THE WESTERN PALEARCTIC. Vol. IV, Terns to Woodpeckers. By Stanley Cramp (chief ed.), Duncan J. Brooks, Euan Dunn, Robert Gillmor, P. A. D. Hollom, Robert Hudson, E. M. Nicholson, M. A. Ogilvie, P. J. S. Olney, C. S. Roselaar, K. E. L. Simmons, K. H. Voous, D. I. M. Wallace, Jan Wattel and M. G. Wilson. Illustrated by Norman Arlott, C. J. F. Coombs, N. W. Cusa, H. Delin, Robert Gillmor, C. E. Talbot Kelly, and D. I. M. Wallace. Oxford Univ. Press, New York, New York, 1985: 960 pp., 98 color plates, numerous range maps, line drawings, sonagrams and diagrams. $98.00.—Volume IV of this magnificent work is every bit as good as its predecessors. The same high standard of scholarship prevails, and the art work is lavish, accurate, and a pleasure to behold. One hundred and thirteen species are covered, completing the nonpasserines; 3 passerine volumes will complete the series. The scope and format remain the same; these are described in detail in my review of Volumes I and II (Wilson Bull. 93:430–432, 1981). The "Field Characters" section seems to be even longer than in previous volumes, sometimes occupying a full page in difficult cases like that of Common Cuckoo (*Cuculus canorus*) and Oriental Cuckoo (*C. saturatus*). Species accounts average about 8 pages, though varying considerably according to degree of knowledge; lengthier treatment is accorded well-known birds like Common Tern (*Sterna hirundo*) (16 pp.), Woodpigeon (*Columba palumbus*) (18 pp.), and Tawny Owl (*Strix aluco*) (21 pp.); but even vagrants like Aleutian Tern (*Sterna aleutica*) (one record, Britain), Yellow-eyed Stock Dove (*Columba eversmanni*) (accidental, U.S.S.R.), and Jacobin Cuckoo (*Clamator jacobinus*) (1 record, Chad) are given 1½–2½ pages and a complete if abbreviated treatment, with field characters, habitat, distribution, movements, voice, etc. The amount of information packed into these volumes is absolutely astounding; nearly 8 pages are devoted solely to the food of the Tawny Owl! The wealth of illustrations of birds in flight, from both above and below, is an extremely valuable feature of this work. As a rule not many races of each species are shown, doubtless for space reasons, exceptions being some of the owls, and I did enjoy finding, tucked in among the variants of the Rock Dove (*Columba livia*), the race *C. l. dakhlae,* endemic to the Dakhla and Kharga oases of Egypt. I continue to find the plate keys somewhat difficult to read, partly because the information is scrunched in so tightly that the eye is easily confused. The problem becomes worse when there are a lot of figures on the plate, and they are not numbered sequentially from top to bottom. I eventually found my way through the maze of swifts on Plate 63 and found what I was

looking for, a Pallid Swift (*Apus pallidus*) drawn from above, correctly showing the contrastingly pale secondaries, and tertials which help to distinguish it from the Common Swift (*A. apus*), conveniently placed next to it on the plate.

A few errors inevitably creep into a work of this size. On Plate 26 there are 28 sandgrouse figures but the plate key only lists the first 12, and on p. 813 we find "*Colaptes auratus*, the Yellow-shafted"—someone forgot to add Flicker. The dotted line showing the regular southern limit in winter of the Snowy Owl (*Nyctea scandiaca*) in North America in noninvasion years is somewhat unambitious, omitting as it does nearly all of New England and much of Alberta. My pet peeve with this work is the complete lack of interest in English names. Whether this is due to inattention, benign neglect, or simply lack of any policy, the attempts to standardize the English names of birds of the world being made in Australia, Africa, North America, and elsewhere have passed completely by the authors of "Birds of the Western Palearctic." In these pages "The" cuckoo, "The" Nightjar, "The" Swift, "The" Kingfisher, and "The" Bee-eater still fly in unmodified splendor, sole proprietors of the family name. The western Palearctic, it would seem, is very resistant to change.

Enough said. Those who own the first 3 volumes of this series will be equally delighted with this one; and those who don't had better buy all 4 volumes quickly before inflation pushes the price even higher.—STUART KEITH.

A CODED WORKBOOK OF BIRDS OF THE WORLD. Vol. 2: Passerines. Second edition. By Ernest P. Edwards. 1986:x + 170 pp., 10 maps. $15.00. (paper cover, plastic binding). (Available from the author, Box AQ, Sweet Briar, Virginia 24595.)—Of lists of the world's birds there seems to be no end. Ernest Edwards who was the author of one of the first (and best) of these lists, has now brought forth a revised (and improved) second edition in two volumes. The first edition of this work, as well as Volume 1 of the second edition, were apparently never reviewed in "The Wilson Bulletin." I will therefore describe the present work in some detail.

The aim of this publication is twofold, to supply a list of names of the world's birds and to devise an alphanumeric code for representing the classification. It is the author's hope that this coding system will be useful for computer entry and other purposes. Besides the list of names, an abbreviated statement about the range is given.

The coding system in the second volume is not the same as the one in the first edition, but represents a distinct improvement of alternating letters and numbers. Quite conveniently Edwards recognizes only 25 orders which are represented by upper-case letters, omitting the letter "O." Hence all the birds in this volume come in order "Z," the Passeriformes. The families are given a number denoting their place in the classification and arrangement that Edwards has adopted. Thus the number 65 represents the family Emberizidae, the 65th in the list. A lower case letter follows, representing the subfamily. The subfamily Emberizinae is letter "c" of this family. This is followed by a number representing the species. Thus as an example, the White-throated Sparrow (*Zonotrichia albicollis*) is listed as "Z65c-56." With a little practice the system is easy to grasp, but I wonder about its eventual adoption by many workers.

The distributional information is also coded. For the White-throated Sparrow the distribution is given as "Hn:c.Can-ne. US/Mex.," which translates to North America (Hn): central Canada to Northeastern U.S./with migrants as far south as Mexico. Such a system obviously works best for nonmigratory species with limited ranges. A set of maps and a list of abbreviations explaining the regional codes are included.

The classification used is that proposed by Cracraft (1981) with some modifications. This

is unfortunate as Cracraft's treatment of the passerines was rather cursory and was admittedly only a hypothesis to be tested. Edwards recognizes 69 families. The enormous family Muscicapidae (of the A.O.U. Check-list) is dismantled into 10 families, restoring amongst others the thrushes and old world warblers to full familial status. The new world warblers, tanagers and icterids are also restored to full family rank. The Carduelinae are considered part of the Emberizidae, which is the old Fringillidae minus *Fringilla.* Most of these changes are defensible, and the dismantling of the Muscicapidae has been carried out in the last volume of the Peters Checklist. However, the results so far published of the DNA hybridization work indicate that many of our present families should be down-graded to subfamilies or even tribes. The last word on classification has yet to be heard.

A comparison with the 1983 A.O.U. Check-list is in order. I count six species recognized by the A.O.U. and not by Edwards, and three recognized by Edwards but not by the A.O.U. In all cases these involved disagreement about the status of geographical variants, subspecies vs species. I counted 37 differences in the scientific names, mostly in generic assignment, and 157 differences in English names, mostly of a trivial nature. These involve Edwards' well-known use of "creeper" rather than treecreeper for the Dendrocolaptidae. Not many readers will be concerned as to whether the members of the genus *Phylidor* are leafgleaners (Edwards) or foliage-gleaners (A.O.U.).

There is also a full discussion of differing taxonomic opinions given in a series of footnotes for each family. But here too the reader must understand a code. Thus typical footnote entry is "Z65b-36 -s.a.b.t. *P. amoena* i.o.m.b.p.o. *P. cyanea* Z65b-35," which tells us that "Some authorities believe the "*P. amoena*" is or may be a part of *P. cyanea.* This information appears to be quite thorough, and to my knowledge no other world list gives any such discussion.

There are four indices: "Genera," "Important Sub-specific Units," "Scientific Names," and "English Names."

In summary, the "Workbook" presents a very workable and usable list of the World's passerine species, together with abbreviated but useful distributional information. Edwards has a reputation of being a careful worker, and the reader can have confidence in the accuracy of the information given. It remains to be seen if the Code for representing the species and their hierarchical arrangement is ultimately used by any number of workers.—George A. Hall.

The Known Birds of North and Middle America. Part 1. By Allan R. Phillips. Privately published, Denver, Colorado. 1986:1xi + 259 pp., 2 color plates, 9 black and white figs. $60.00. (Obtainable from Dept. Zoology, Denver Museum of Natural History, City Park, Denver, Colorado 80205.)—There are those who complain that present-day scientific writing is "dry as dust" and generally lacks any personality. The volume at hand is certainly an antidote to that accusation. As might have been expected from Allan Phillips the present work is idiosyncratic, peppery, not to say polemical, but for all of that a contribution worth examining. The work represents the first part of Phillips' personal "Check-list" giving, according to the subtitle, "Distributions and Variation, Migrations, Changes, Hybrids, etc." of the "known" birds. The "known" emphasizes Phillips' well-taken point that a title such as "The Birds of Ruritania" implies that nothing more is to be learned about the avifauna of that area. Phillips feels that there is much yet to learned about the birds of North and Middle America, and indeed claims to have seen briefly several birds not known to be described anywhere.

This book covers only the first few families in the Oscine list as given by the Wetmore order: Hirundinidae, Corvidae, Laniidae, Paridae, Aegithalidae, Remizidae, Sittidae, Trog-

lodytidae, Cinclidae, Pycnonotidae, Timaliidae, Mimidae, and Certhiidae. The area covered differs somewhat from that covered in the Sixth Edition of the A.O.U. Check-list in that Phillips includes Greenland and Cuba (but not the rest of the West Indies), along with the North American continent south to Panama, while the A.O.U. omits Greenland, but includes the Indies and Hawaii. I have compared carefully the two lists for the area they both include and find that Phillips recognizes 145 species in this area while the A.O.U. recognizes 143 (including additions made in the 1985 supplement). I will take up the differences later.

The list cannot be appreciated fully without an understanding of Phillips' strongly held opinions, his prejudices, and his *bêtes noires,* of which the reader will soon be well-aware after reading the 61-page Introduction. There are too many to enumerate them all here, but I mention three of his most prominent ones. He has no use for the A.O.U. Committee on Classification and Nomenclature, which he refers to simply as the "AOU" or often as the "Eisenmann/AOU." In particular he is vociferous and caustic about some of the changes in English names made in the recent list, a view shared by countless "birders." The International Commission on Zoological Nomenclature is constantly taken to task for its abandonment of strict priority in its use of *nomina oblita.* Finally it seems that nothing that emerges from Berkeley's Museum of Vertebrate Zoology can have any scientific merit whatsoever. The transgressions of these groups, and others, are pointed out and discussed at great length, repeatedly, and frequently to the point of boredom on the part of the reader.

Phillips does not recognize *Progne cryptoleuca, P. sinaloae, Calocitta colliei, Pica nuttalli,* and *Mimus gilvus* accepted by the A.O.U. Check-list. On the other side he grants specific status to *Stelgidopteryx ridgwayi, Corvus sinaloae, Troglodytes beani, Thryothorus albinucha,* and *Mimus magnirostris,* all considered to be subspecies by the Check-list Committee. Besides these Phillips sinks *Aphelocoma coerulescens,* dividing it into three species, *A. floridana, A. californica* (which includes the *woodhouseii* group of the A.O.U.), and *A. insularis.* None of these differences is very radical, as in all cases the A.O.U. Committee discusses these possibilities in the "Notes" section of the various species.

There are several differences in scientific names, the most variant being the assignment of the Gray Catbird (*Dumetella carolinensis*) to the genus *Lucar,* and the use of the specific names *albifrons* for the Cliff Swallow (*Hirundo pyrrhonota*) and *domesticus* for the House Wren (*Troglodytes aedon*). The other differences come largely from the different criteria for generic recognition. In the matter of English names Phillips is a traditionalist and generally prefers the names that date from the 1931 Check-list, even when these were applicable to only one subspecies.

One advantage the "Known Birds" has over the Check-list is the extent of the documentation. In the Check-list it is often difficult to determine why the Committee made such and such a taxonomic decision, but Phillips has been assiduous in giving references, although his system is not the easiest to use and there is no terminal bibliography.

The major contributions of this work are two. Phillips has presented some detailed distributional data that in some cases disagrees with the material in the A.O.U. Check-list. The disagreement is particularly noticeable in the Middle American species which have occupied Phillips for so many years. These differences deserve careful attention, an in many cases Phillips points out where good knowledge is lacking. The other contribution comes from the careful attention to geographic variation and the description of subspecies. The 1983 Check-list omitted the discussion of subspecies, but we are told that the Committee on Classification and Nomenclature is working on a full-scale treatment of these. This Committee will certainly have to take Phillips' material into consideration. Subspecies are now considered to be *passé* by many ornithologists, and one of the continuing sermons in Phillips' book takes to task those of such persuasion. Phillips has enlisted the help of Robert W. Dickerman, Amadeo M. Rea, and J. Dan Webster for taxonomic treatment of certain

species or parts of species. Indeed, an appendix gives a detailed and exemplary review of *Certhia americana* by Webster. Phillips places the family Certhiidae as *incertae sedis.* Three other appendices by Rea present basic data on *Corvus* and *Lanius.*

The long introduction deserves reading by all ornithologists. Of course one must accept and allow for the polemics, but the message is valuable. Much of this introduction is devoted to an advocacy of further collection of specimens. Of special interest are his remarks about the absurdity of the claim by permit granting agencies that collecting must be controlled for the conservation of birds. Phillips discusses in detail (sometimes too much detail) the fact that existing museum collections have in many cases deteriorated too much to be useful for studies of color variation. The sections on "Why we can *not* trust our eyes in science" and "Problems in the use of museum specimens" should be required reading for all those who feel that the collecting of specimens is no longer needed either for assuring proper identification of rarities or for adding to museum series.

The text would have benefited from tighter editing. Phillips sometimes goes out of his way to castigate someone who disagrees with him, and while many of his fulminations are interesting, they are often repeated too many times and in too many irrelevant places. He frequently calls an opinion or statement unscientific, but it seems to me that Phillips himself is unscientific in arbitrarily rejecting all results of modern techniques of studying avian classification.

The book is handsomely published and is apparently free of typographical errors. The map labeled "Distribution of American *Corvus corax*" omits all of the eastern occurrences.

The work is graced by two colorplates by Anne Pulich, showing the *Stelgidopteryx* swallows and the *Microcerculus* wrens.—George A. Hall.

The Encyclopedia of Birds. By Christopher M. Perrins and Alex L. A. Middleton (eds.). Facts on File Publications, New York, New York, 1985:xxxi + 447 pp., heavily illustrated with color artwork panels and photos, small range maps. $35.00.—This sort of general compendium has been done repeatedly over the last few decades, but seldom so well. The reasonable price is a bonus. The title is a little misleading for the book is more an encyclopedia of bird *groups*—usually families or orders. The text is written by 88 expert contributors: 46 from Great Britain; 19 from the U.S. and Canada; 14 from Australia and New Zealand; and 9 variously from Europe, South Africa, Costa Rica, and Malaysia. Curiously, Alex Middleton does not appear in the list of contributors, although he is co-editor with Perrins.

The book begins with a short "Preface" and "Notes on Classification" by Perrins. As is appropriate in a work for the general reader, there are no taxonomic breakthroughs here, with the classification based "with few exceptions, on the so-called Wetmore order which is used in [Peters' *Check-List*]"! The number of species in each family is that of Gruson's "Checklist." One could raise an eyebrow at the editorial discretion here, but that might be quibbling, in view of the general excellence of the text.

The body of the book is introduced by a general chapter on avian biology by Perrins—14 pages outlining bird evolution, the fossil record, physiology, anatomy (including plumage and with an emphasis on flight adaptations), breeding biology, and behavior. The main text is arranged in taxonomic order and blocked out in three parts of approximately equal length: ostriches to button quails, plovers to woodpeckers, and passerines. Each of the 66 group entries is organized into a general text discussion of physical features, distribution, evolutionary history, classification, breeding biology, diet and feeding behavior, social dynamics and spatial organization, conservation problems, and relationships with man (with modifications of this format, as appropriate). Each group (usually a family but occasionally orders, suborders, or subfamilies, depending on their size) is given an information panel or side

bar that provides a factual condensation of the formal classification, the number of genera and species, the main distribution (also shown on a small outline map of the world), the habitat in which the birds are found, their body dimensions (including weights and a system of silhouettes of the largest and smallest species scaled against a human figure—entire, legs, head, or foot), plumage, voice, nests, eggs, diet, and a list of representative species with both English and scientific names. On some pages are special boxes for discussions of particular features of a group such as the courtship displays of bustards, lead poisoning of waterfowl, hornbills in human cultures, and cooperative breeding in babblers. These special boxes offer some of the most interesting reading in the book.

In addition to their fine assembly of authors, the editors have enlisted the talents of 10 excellent artists, including one of my personal favorites, Robert Gillmor. Each entry is well illustrated with a variety of color artwork, usually showing the range of types found in the group, and many also have black-and-white drawings of behavioral specialties such as a blackbird "gaping" for food in vegetation, various courtship sequences, pelicans diving for food, and the changes in dry vs soaked belly feathers in sandgrouse. There are also many color photographs: most are excellent, some are magnificent, a few are just adequate. The color reproduction is superb and the page design both pleasing to the eye and well organized as to content.

The only serious negative aspect I found in this book was the short shrift given to certain, especially New World, groups: The tinamous (46 spp.) are allotted only 1 page of text (and a full-page photo of the front end of a crouched *Crypturellus* that adds little), but the next order, penguins (16 spp.), receives 10 pages; the pigeons (300 spp.) get only 4 pages, whereas auks (22 spp.) get 8. Some very large groups are also skimped: the (mostly) New World "suboscines" (1065 spp.) are granted just 20 pages (in 4 groups), the Muscicapidae (1394 spp.) have 18 pages, and the starlings-orioles-drongos (154 spp.) get only 4, while the Falconiformes (286 spp.) have 24 pages. Granted, more is known about some birds than others, but much is available that could have been included—I'm sure that John Fitzpatrick and David Snow could have written a great deal more than 1½ and 2 pages, respectively, on tyrant flycatchers and manakins-cotingas, given the space by the editors. Unfortunately, this sort of bias is common in books of this nature, but I was disappointed to see it in an otherwise fine book. On the other hand, I was pleased by the clear effort not to overemphasize European species—a tendency common in books produced by European companies (this one is credited to Equinox [Oxford] Ltd.). The availability of high quality photographs must make it very tempting to use the output of local photographers rather than make the effort to find less commonly illustrated species.

I found no statement that this title was designed for publication in several countries but it almost surely was. In any case, American readers will find only a few "Britishisms" that made it into the American edition: "darters" rather than "anhingas," and an American Whip-poor-will (*Caprimulgus vociferus*) was "ringed" rather than "banded" (p. 248), but Gaviidae are "loons" *or* "divers."

The book concludes with 2 pages of bibliography and art and picture credits, a 2-page glossary, and a 12-page index (the last printed in vanishingly small type, a tendency I've noticed lately in large-format British publications). The proofreading was meticulous (I noticed only one error and that probably was editorial rather than typographical—"Motmotidae" (p. 270, twice) but, correctly, *Momotus*. In no case did I find a vernacular name that was not accompanied, somewhere in the account, by its scientific equivalent.

Although it is the duty of a reviewer to point out the shortcomings of a book, none of my criticisms should alter the conclusion that this is a *superb* book for its type, and the price makes it a bargain addition to any library—professional or otherwise.—MARY H. CLENCH.

A Field Guide to the Birds of Colombia. By Steven L. Hilty and William L. Brown, illus. by Guy Tudor, H. Wayne Trimm, John Gwynne, Larry McQueen, John Yrizarry, P. Prall, and Michael Kleinbaum. Princeton Univ. Press, Princeton, New Jersey, 1986:836 pp., 56 color plates, 13 half-tone plates, 100 line drawings, 11 photos, 1 table and 1475 range maps. $45.00 (paper), $95.00 (cloth).—This monumental book is the latest in a series of field guides that reflect the extent to which our knowledge of South American birds has increased since the publication in 1964 of Meyer de Schauensee's landmark "The Birds of Colombia" (Livingston Press, Narberth, Pennsylvania). Hilty and Brown have compiled an extraordinary amount of information on each species including their field identification, vocalizations, behavior, and breeding in addition to the more typical information on plumage, status, habitat, and range. There are also 1475 range maps and a guide to finding birds in Colombia. These details set this guide apart from all other South American guides; clearly, it was written by and for field-oriented ornithologists and bird-watchers.

The plates, including 47 by Guy Tudor, are superb, and line drawings fill many of the gaps in coverage. The majority of the paintings are borrowed from two other Princeton Univ. Press field guides, "A Guide to the Birds of Venezuela" (Meyer de Schauensee and Phelps 1978) and "A Guide to the Birds of Panama" (Ridgely 1976). There are, however, several new plates, and Colombian species not found in Panama and Venezuela have been added to the older plates. The result is that nearly all resident birds are illustrated. The two new tanager plates by Guy Tudor (Nos. 48 and 50) are especially beautiful. As usual, most Nearctic migrants are not shown.

Range maps at the end of the book are extraordinarily detailed and will be useful for ornithologists and birders visiting Colombia and also for biogeographers. Hilty and Brown have been especially careful in showing the ranges of species with narrow elevational distributions.

The text of the book is well planned and executed. The introductory section includes clear definitions of terms, an explanation of the complex topography and climate of Colombia, descriptions of the major habitats, a section on migrants, a brief discussion of conservation problems, and the history of Colombian ornithology. I found the habitat descriptions to be especially useful—few previous field guides have presented such detailed information on bird habitats. Hilty and Brown clearly appreciate the important distinctions between *varzea* (seasonally flooded) and *terra firme* (above flood level) forest in the Amazonian section of Colombia.

Species accounts contain a wealth of detail that facilitates identification while at the same time providing information of use to researchers. I found the "similar species" section to be quite useful in the field. The addition of this section as well as the more extensive use of italics for diagnostic characteristics represent a major advancement over the other South American field guides. The details on voice and behavior show how carefully Hilty and Brown researched each species. In addition to references to the published literature, there are many unpublished observations by the authors and by other field workers such as Ted Parker, Van Remsen, Tom Schulenberg, John Fitzpatrick, and Robert Ridgely among others. The authors also made extensive use of their own recordings and those of the Laboratory of Ornithology's Library of Natural Sounds, including many by the late Paul Schwartz. As a result, a great deal of natural history information is presented in this book for the first time. I was amazed, for example, to find a detailed account of the behavior and voice of the Black Bushbird (*Neoctantes niger*), a bird I had always thought was essentially unknown outside of a few scattered specimens. Hilty and Brown state that Black Bushbirds "often peck and chisel fallen rotting logs somewhat like a piculet" and are found "inside or at the edge of humid *terra firme* and *varzea* forest, esp. in log-scattered swamps or creek borders

. . . ." Details such as these make for fascinating reading and clearly demonstrate the authors' vast field experience with even the most obscure and secretive species.

The field guide is large, which makes it rather cumbersome to use in the field, but large size is unavoidable when dealing with a fauna of 1700 species. Unlike "A Guide to the Birds of Venezuela," which tends to fall apart after a few months in the field, this guide is well bound. All three paperback copies we took to Peru last fall survived intact 4 months of nearly continuous use. Apparently, Princeton Univ. Press has learned from their previous experiences and greatly improved the binding to withstand field conditions. The hardback, which is also unusually expensive, is printed on acid-free paper, which should increase durability. The reproduction of the color plates in the copies I have seen has been excellent. I hope that funds can be found to translate the guide into Spanish.

"A Field Guide to The Birds of Colombia" incorporates the best features of the publisher's two other Neotropical field guides. It combines the best of the artwork of "A Guide to The Birds of Venezuela" with the detailed field-oriented text of "A Guide to The Birds of Panama." This book is and will continue to be essential for everyone visiting the Neotropics and for collectors of bird books. I feel that this book is worth the money, which is high praise indeed for such an expensive book.—Scott K. Robinson.

The Atlas of Australian Birds. By M. Blakers, S. J. H. F. Davies, and P. N. Reilly (eds.). Melbourne Univ. Press and the Royal Australian Ornithologists' Union, Melbourne, Australia, 1984:738 pp., 782 distributional maps, 648 vignettes of birds. $54.00 (Australian).—This comprehensive distributional atlas (page measurements 11 × 8 in., range maps of 6 × 6 in.) is the result of a cooperative project involving 300 field workers (90% of them amateurs). It is the result of four years of concentrated work which involved both repeated assessments in better known areas and the mounting of a series of expeditions to remote places to fill in the gaps. There is a Bibliography of 1929 titles. Breeding and nonbreeding distributions are shown separately. An endeavour is made to get data on historic changes in bird distributions and abundances by treating the data at three levels: (1) records prior to 1901 (plotted on smaller maps at the back), (2) 1901–1950, and (3) 1951–1976. The first is obviously much less complete than desired. Already, by the turn of the century rabbits and sheep had greatly modified Australian habitats. We have good data prior to 1900 for only for a few select areas. But these, the 1901–1950 data, and recent work does confirm considerable distributional and numerical changes, with many of the more interesting species becoming rare and others (that thrive with clearing) both increasing their ranges and becoming much more abundant. Documentation of this is one of the great achievements of the Australian atlas. The second achievement is the provision of a series of modern distribution maps of all the Australian bird species. The third is to bring out the occurrence of a range of previously unsuspected seasonal shifts in distribution in many species (i.e., differences in breeding and nonbreeding areas of concentration).

In developing the atlas the following procedures were followed. Data were plotted on maps of the continent with 1° grids (giving a total of 885 blocks). For insular Tasmania the blocks were 10 min. For better-known areas several dozen sheets were compiled compared to one or two for remote places. Bias was minimized by adjusting for such differences in reporting rates.

The atlas is enlivened with a 400–500 page account of the biology of each bird species, and with a series of small black-and-white vignettes. Hence in more ways than one it is an invaluable document. One can only wish the R.A.O.U. luck with their follow-up project, developing data on abundances of the various bird species in different areas.—Allen Keast.

THREATENED BIRDS OF AFRICA AND RELATED ISLANDS. By N. J. Collar and S. N. Stuart. Int. Council for Bird Preserv. and Int. Union for Conserv. Nature and Nat. Resources, Cambridge, England, 1985:xxxiv + 761 pp., 12 color plates. £24 ($45.00 from Buteo Books, Vermillion, South Dakota).—Listed on its cover as "The ICBP/IUCN Red Data Book Part 1," this volume treats in comprehensive, if summary, detail the endangered, threatened, and possibly threatened birds of Africa and such outlying islands as Madagascar! Discussed fully are 172 "threatened" species (plus 1 "Out-of-Danger" and 4 "Of Special Concern"), more briefly 93 "near-threatened" species, 16 "threatened" or "near-threatened" incipient species, and 23 or 24 species whose main range falls outside the region and will be covered more fully in subsequent "parts" (on the Americas, Eurasia, Australasia, and the Pacific, etc.). For each threatened species there are these sections: "Summary," "Distribution," "Population," "Ecology," "Threats," "Conservation Measures Taken," "Conservation Measures Proposed," and sometimes, "Remarks," as well as references. Most accounts are several pages in length, but there are 35 pages on the Northern Bald Ibis (*Geronticus eremita*), which really is a Mediterranean species. The accounts are generally excellent, and provide in capsule form a host of information on the biology of these species, with extensive, up-to-date references. The book is a tribute to the many contacts within (and outside) Africa made by I.C.B.P., I.U.C.N., and the authors.

Where evidence is indicated, no holds are barred in calling attention to the sources of threats. In one sense the book is too up-to-date, for between the lines are indicted some governments and agencies in Africa which are continuing or expanding upon some faulty colonial programs. Most "threats" have a long history of development initiated in colonial times. It is no wonder that we cannot and must not urge preservation upon African nations for abstruse, philosophical, or long-term practical reasons—preservation simply has to make sense economically, in the short term.

Naturally a great proportion (44%) of threatened species are on islands, usually relatively small in area and having faced a long history of human interference with ecosystems. Some 28 such species are on Madagascar and 20 in the Mascarenes, Seychelles, and Aldabra. Although two species have not been seen in 50–100 years, there is as yet no documented extinction in recent times on the African mainland. Don't hold your breath, though—65% of the tropical African or Afrotropical threatened species are dependent upon forests, and it is the forests that are disappearing and changing most rapidly, involving the very avifaunas most susceptible to subtle let alone massive changes. The authors pinpoint five areas of special concern that involve 92% of the threatened forest species: the Upper Guinea Forest, the montane and lowland forests of western and southern Cameroun (both an area of endemism and a faunal exchange area), the western scarp of troubled Angola, lowland and mountain forests from southwestern Uganda and Rwanda to adjacent Zaire ("Albertine Rift"), and the pitiful remnant of eastern Kenyan and Tanzanian forests. Some of these forests, of which little is left, are going fast (e.g., Mount Nimba's forests in West Africa and Sokoke Forest in eastern Kenya). Yet I suspect that when more data are available, nonforest avifaunas will be shown increasingly and severely threatened by the kinds of changes (desertification, firewood gathering, grazing in marginal lands) now taking place wholesale. The problems of some nonforest birds are masked by apparently wide distributions, but habitat fragmentation and degradation could make many such species threatened soon.

One can question some inclusions of material, and page space given to species that have been studied extensively (on islands especially), and are covered in prior I.C.B.P. reports. Some of these species (e.g., Mauritius Kestrel, [*Falco punctatus*]) are represented by tiny populations and have relatively little chance of increase in the wild, given human activities and lack of habitat. Norman Arlott's usually good paintings grace the book—but they increase

its price, and thus directly cut into its distribution among African wildlife workers who need just this sort of book. (It is even expensive for those inevitably underpaid expatriot ornithologists trying so hard to help in the African countries.)

I could quibble philosophically about conservation's impingement upon science in the case of the broadened biological species concept the authors favor. By excluding megasubspecies from consideration, they are prone, as they state in the Introduction, to raise to species status some such forms and very questionable species (one frequently sees threatened species noted as "often considered subspecies of"). We should educate about what species are, how they evolve, and how important to their long-term survival are genetically distinct populations (subspecies or not!). But I don't want to belabor the authors for the fine job they have done, in a limited time (a bit over 3 years). They have set a high standard for the other "parts" of the Red Data Book, the next of which (on the Americas) is due out soon.

I recommend this book highly to all concerned amateur and professional ornithologists (all of whom *ought* to be "concerned"), for it well attests to the variety and severity of the threats to birds (and ultimately to our science, which depends upon them, and even to us) the world over, but especially in the tropics, where there are the most birds to lose.—LESTER L. SHORT.

ECOLOGY AND MANAGEMENT OF THE SPOTTED OWL IN THE PACIFIC NORTHWEST. By Ralph J. Gutierrez and Andrew B. Carey (eds.). U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW-185, Portland, Oregon, 1984: 119 pp., 8 numbered text figs., 18 tables. No charge.—The Spotted Owl (*Strix occidentalis*) has become a controversial species in the Pacific Northwest because of its association with old-growth Douglas-fir (*Pseudotsuga menziesii*) forests—forests which are the focus of considerable lumbering activities. Prior to 1970, the owl was thought to be "rare" or "uncommon." In the late sixties Eric Forsman began studies of the owl in Oregon (I had the pleasure of participating in those studies), and by 1970 it was clear that populations of the owl were being decimated by tree harvests, and indeed, that old-growth Douglas-fir forests were themselves threatened. Numerous attempts to bring the plight of the owl to the attention of forest and wildlife management agencies generated enough interest to initiate Gordon Gould's survey of Spotted Owls in California in 1973. Forsman's and Gould's findings resulted in a rapid expansion of studies of the owl throughout most of its range. Many of these studies are included in this book, which is the proceedings of the Symposium on the Ecology and Management of the Spotted Owl in the Pacific Northwest, held at the 54th Annual Meeting of the Cooper Ornithological Society in Arcata, California (1984). The stated purpose of the symposium was to bring concerns about Spotted Owls before public and scientific scrutiny. Papers in the book are grouped into three sections: (1) "Management" (8 papers)—consisting of contributions by various agency personnel specifying the history of their concerns for the owl, the laws and regulations which govern management activities, and the status and specifics of various Spotted Owl management programs; (2) "Research" (7 papers)—including two overviews of Spotted Owl research, and others on the owl's diet, the sizes of their home ranges and composition of forests within ranges, juvenile dispersal, and winter migration; and (c) "Theoretical" (2 papers)—one on the demography and population genetics of the owl and another on its meta-population and conservation.

In the management section readers get a fair understanding of how the resource agencies (U.S. Forest Service, Washington Department of Game, Oregon Department of Fish and Game, California Department of Fish and Game—missing was a contribution from the Bureau of Land Management) are dealing with the Spotted Owl. The principal concern

among agencies is locating habitats, either occupied or presumed suitable for supporting a pair of owls, and to exclude some acceptable number and distribution of these from tree harvest. A shortcoming of the management plans described is the emphasis on the enumeration of habitat rather than on the actual numbers of owls. Although several papers in this section are difficult to read because of inconsistent use of terms and abundant jargon, several papers, notably those by Gould and Beckstead, are quite informative in that they contain considerable data on the distribution of owls in California and Washington—these authors obviously spent a great deal of time in the woods.

The research section begins with Gutierrez's overview of research on the owl and the extent of knowledge of its natural history, ecology, and demography. Also discussed are five hypotheses as to the owl's affinity for old-growth forests. Cameron Barrows presents limited data on the diets of owls in California, and suggests that the irregular nesting of Spotted Owls (a trait of the owl throughout its range) is related to the availability of large mammalian prey e.g., *Glaucomys* and *Neotoma*). Allen and Brewer review the current owl research in the state of Washington (all of which is in early stages) and give preliminary data on habitat and juvenile dispersal. Forsman and Meslow present the acreage of old-growth forest within the home ranges of six pairs of radio-tagged owls in Oregon. Gutierrez et al. present data on natal dispersal in California, showing that dispersing owlets move rapidly (8 km/day) and that mortality during dispersal is high. Miller and Meslow also report low survival among dispersing owlets in Oregon. In the final research paper, Laymon reports that adult Spotted Owls in the Sierra Nevada migrate downslope to winter in foothill habitat, a fact that will certainly complicate the management of the owl in California.

In the theoretical section, Barrowclough and Coats use the meager life-history data available on the owl to estimate the effects of habitat depletion (and loss of owls) on the owl's effective population size. Shaffer introduces the concept of the meta-population (populations of populations) for understanding the extinction-persistence dynamics of species that are patchily distributed and whose patchwork of habitat is being altered. In this endeavor he considers the number, size, and distribution of Spotted Owl management areas (preserved old-growth Douglas-fir stands presumed suitable for one or more pairs), the proportion of these areas occupied by owls, and the proportion receiving dispersants and losing owls through extinction. In addition, the theoretical effects of demographic, environmental, and genetic stochasticity, with respect to decreasing population size, are analyzed. The important contribution of the theoretical papers is the identification of empirical and theoretical areas of research needed to refine models of the owl's population dynamics. In the penultimate paper, the concepts, information needs, and management options identified during the symposium are nicely reviewed by Carey. Why the last paper, another review of the symposium by Gutierrez, is included is not clear as it is mostly a reiteration of Carey's.

This book contains most of the up-to-date information on the ecology and management of Spotted Owls. Many of the papers, however, give results that are incomplete or that are based on small samples. As a result, the reader is left with the disheartening feeling that management of the owl is predicated on critically little knowledge of its life history. The book will primarily be used by resource managers and students of Spotted Owls, although ornithologists interested in other strigiforms will also find some useful information in the book.—RICHARD T. REYNOLDS.

THE LINGUAL APPARATUS OF THE AFRICAN GREY PARROT, *PSITTACUS ERITHACUS* LINNE (AVES: PSITTACIDAE): DESCRIPTION AND THEORETICAL MECHANICAL ANALYSIS. By Dominique G. Homberger. Ornithol. Monogr. 39, American Ornithologists' Union, Washington, D.C., 1986:xi + 233 pp., 64 black-and-white figs., 23 tables, 2 appendices. $25.00 ($20.00 for

A.O.U. members).—The fleshy, manipulative tongue of parrots is much more complex than that of most birds. In this monograph Homberger shows that it is even more complicated than previously believed, providing a thorough analysis of the lingual mechanism in a single species, which is intended to serve as the basis for further comparative studies. The work is divided into two major sections, descriptive and analytical. The first part is a very detailed description of the anatomy of the lingual apparatus in the African Grey Parrot, (*Psittacus erithacus*). Emphasis is placed on the hyoid skeleton, including its articulations, ligaments and fasciae, musculature, synovial bursae, surface features of the tongue, and salivary glands. Neural and vascular structures are examined less critically because they do not contribute to the mobility of the system, except for certain expansible cavernous vascular tissues. These descriptions are long and detailed, and only committed anatomists will want to read them closely. Nevertheless they constitute the necessary data base for this and future studies, and the publication of such material in extended form fulfills an important archival function of series like the Ornithological Monographs. The descriptive text is augmented and illuminated by many excellent halftones and line drawings that illustrate structural details from a variety of views.

The specializations of the parrot tongue include an unusually massive hyoid skeleton with highly complex articular surfaces. Muscles that are simple in most birds become split into separate divisions, sometimes distinct enough to constitute new muscles. Functional versatility is further enhanced by unique hydraulic structures in the salivary glands and corpora cavernosa.

The second part of the study is a functional analysis of the lingual apparatus based upon the descriptive material. The approach taken is to construct conceptual models of the functioning of several subsystems and to integrate these into a theory of the overall activity. The various movements within the apparatus (e.g., "back-and-forth movement of the hyoid," "up-and-down movement of the paraglossale," "movements of the epithelial surfaces of the tip of the tongue," etc.) are inferred from the descriptive material of the first section. This analysis is carried out within the framework of a "Theoretical Mechanical Model" synthesized from (1) the physical and physiological properties of various tissues and (2) general biomechanical principles. The model is developed before the specific analysis of *Psittacus* is presented. It provides rigor and constraint to the process of functional speculation, holding it within the bounds of the known properties of supporting and connective tissues, muscles, epithelia, and hydraulic structures. On the other hand, the possibility of oversimplification must also be considered; as Homberger states, the model is not quantitative and cannot make quantitative predictions about movements and forces.

Within the limits of this approach Homberger's functional analysis involves a detailed series of hypotheses about how the movements of the tongue, including its changes in shape, are brought about through the actions of the mechanisms first described and then interpreted under the Theoretical Model. These are presented, perhaps, in more confidently declarative fashion then their speculative nature warrants, but this is a criticism more of style than of substance.

This study was intended to serve (1) as a basis for future anatomical investigation of the avian feeding apparatus, (2) as a foundation for future evolutionary analyses of parrot feeding, and (3) as an example of a certain approach to functional analysis. Its reference value for the first point is assured. The ultimate success of the approach will depend on how effectively the program proposed in the second point is carried out. Fundamentally, it will succeed or fail on the degree to which its predictions are corroborated by experimental analyses of the system by such techniques as electromyography and cineradiography. Homberger stresses this testable nature of her approach. In addition, the value of the method will rest in part on the extent to which it can provide an insight into the phylogeny and adaptive radiation

of the parrots and other groups. The application of functional methods to phylogenetic analysis is a controversial area, and it will be of interest to see how the analysis of biomechanical systems might be applied to the determination of evolutionary directionality.

Thus, Homberger's monograph may be taken to be (1) a valuable descriptive study of the lingual apparatus in a representative species of parrot, (2) an example of a method of functional analysis whose purported strengths require and are amenable to empirical verification, and (3) the possible basis for a broader evolutionary study whose methods and premises are as yet largely undefined. Anatomists and systematists will look forward with interest to the future development of this ambitious research program.—ROBERT J. RAIKOW.

CROWS OF THE WORLD. 2nd ed. By Derek Goodwin, illus. by Robert Gillmor. St. Edmundsbury Press Ltd., Bury St., Edmunds, Suffolk, England 1986:299 pp., 6 color plates, numerous line drawings and range maps. £30.—The first edition of this book, published in 1976, appeared appropriately during a renewed wave of interest in the study of the Corvidae, particularly in Australia, Europe, and North America. Basic biology and an understanding of the ecological underpinnings of various exploitation systems formed the main substance of these studies. Goodwin's first book together with Coomb's "The Crows, a Study of the Corvids of Europe" (1978), provided a stimulus to further study. A perusal of the recent literature shows that the wave of interest in the study of this fascinating group of birds has by no means reached its crest.

The book is divided into 9 chapters, of which the first 8 provide a brief (47 pages, printed in double columns) but sufficiently detailed overview of corvid biology. The first 3 chapters deal with nomenclature and relationships within this diverse group of birds, adaptive radiation and adaptive characters, and plumage and coloration. The 6 color plates show 30 species and subspecies, and they add much to the attractiveness of the book and to an appreciation of the inter- and intraspecific diversity of the Corvidae. In the chapter on maintenance behavior, Goodwin deals with feeding habits (not food), food storage, and maintenance of the feathers. Chapter 5, on social behavior and display, takes up 14 pages and provides a good general review of, among others, flocking, territory, roosting, pairbond, and communication. Relatively little space is devoted to nesting and parental care in Chapter 6 and proportionally much space in Chapter 7 to voice and vocal mimicry, which reveals Goodwin's own interests. The last overview chapter deals with escape, mobbing, and some other kinds of antipredator behavior, and it brings out many interesting facts. Each of these first 8 chapters has a brief list of references (a few up to 1984, some rather ancient). Many of us will look in vain for our own contributions to the corvid literature. To those who may be wounded by this, I should add that a more complete review of the literature was beyond the scope of this book. Throughout these first 8 chapters Goodwin relies on his considerable personal knowledge of wild and captive species of corvids which gives the book an authoritative ring.

The remaining 239 pages of the book are devoted to species accounts of all the corvid species in the world. Each major group of species, such as "The typical crows" and "The American jays" is preceded by a general discussion dealing with taxonomy, ecology, and behavior of the group. In reading these accounts, it soon becomes apparent that much is known about some species and little to nothing about most others. Many of the species are depicted in perceptive pen and ink drawings, and for all species very rough range maps are shown, which have some species occurring rather far out at sea! This sloppiness could have been avoided. The map of the Steller's Jay (*Cyanocitta stelleri*) is clearly wrong. When available, each species account closes with one or more references.

The value of this book is twofold. It brings together enough of the corvid literature to

serve as a source book of the behavior and ecology of this group of birds and it points out the gaps in our knowledge, particularly obvious in the species accounts. Our lack of knowledge pertains particularly to species in remote parts of the world. However, it may be useful to mention that close to home the breeding biology information provided for the Gray Jay (*Perisoreus canadensis*), Steller's Jay, American Crow (*Corvus brachyrhynchos*), Fish Crow (*C. ossifragus*), and Chihuahuan Raven (*C. cryptoleucus*), is largely based on Bent's "Life Histories of North American Jays, Crows and Magpies" (1946)! Lots of potential thesis material here.

Rather than dwell on the imperfections of this book, some of which have been pointed out, and which collectively are a minor blemish, I would like to stress that this is a well written, authoritative book. A real thorough synthesis of corvid biology will have to wait to a later date. If you do own the 1st edition you may not want to buy the 2nd one as it does not include that much new information. If you do not own the 1st edition, the 2nd one is certainly well worth having.—NICOLAAS A. M. VERBEEK.

A WORLD OF WATCHERS. By Joseph Kastner. Alfred A. Knopf, New York, New York, 1986:241 pp., 8 color plates. $25.00.—This is an anecdotal history of American ornithology, tracing the roots of the modern boom in birding through the lives of people who contributed significantly to it from Alexander Wilson and John James Audubon and their predecessors down to Roger Tory Peterson.

Kastner is a good story teller, and the emphasis is on details of human interest rather than the sweep of history. Nevertheless, he sees American bird watching, as distinct from scientific ornithology, falling into three periods: first, the time of Spencer Fullerton Baird and William Brewster in the 19th century and spilling over into this one when watchers' efforts were coordinated for the first time; second, the early years of this century when the Audubon Societies popularized birds and spread the gospel of bird protection; and third, the present time, which he designated the era of the bird guide.

Along the way he brings back nearly forgotten controversies that now seem amusing but at the time generated considerable heat. One was the debate over the villainy of the House Sparrow (*Passer domesticus*). The sparrow lost, and bounties were put on it in some places. Another was the argument about taking scientific specimens, with old-timers who formerly collected now arguing that the younger generation should be curbed. The protectionists won a partial victory, and collecting was sharply curtailed by law. Ironically, although Kastner does not note it, this debate occurred just about the time there was an increasing need for study specimens in schools and museums, spurred in part by new statistical methods and the pursuit of subspecies calling for large series of specimens. Lately, new biochemical approaches to taxonomy require the gathering of fresh material.

There is, I believe, a distinction that can be drawn between people who look at birds to discover truths about them, and those who are simply chasing rarities and looking merely to be entertained. Also there is a distinction between professionals who earn livings through their study and amateurs whose work with birds is outside their regular occupations, but these classifications become tenuous, as nearly all scientists in ornithology began as bird watchers. However, Kastner does not concern himself with these distinctions, and he gives attention to all types—the giants of American ornithology like Baird and Elliott Coues; the celebrities who were in the public eye for other reasons like the two Roosevelts, Henry Ford, and Nathan Leopold; and obscure individuals whose influence scarcely reached beyond their own communities.

The major focus is on the last century, and Kastner does not dwell on famous scientific figures of our time except for Margaret Morse Nice. He does, however, treat the principal

ornithological societies (American Ornithologists' Union, Wilson Ornithological Society, and Cooper Ornithological Society) with particular attention to long-forgotten squabbles of the early days. Having held office in all three over several decades, I can speak as an insider and say I have not sensed any of the resentment of the Eastern establishment that Kastner highlights. It is true than in the beginning the A.O.U. was in the hands of men attached to the great museums of the Washington-Philadelphia-New York-Boston axis, but for a long time now the "New York dominance" Kastner mentions has not been apparent in the leadership, papers published, attendance at meetings, nor published biographies of members.

In discussing these societies, Kastner, I believe, plays up regionalism, which is largely past history. Today all the distinctions are minor, with the A.O.U. perhaps favored by museum workers but attempting universal coverage of ornithology, the Wilson Society still favoring field studies of the living bird, and the Cooper Society particularly represented by laboratory experimenters and by field workers in Latin America and Alaska. The influential "Journal of Field Ornithology" (formerly "Bird-Banding") is not mentioned in this book although it has been in existence more than half a century. Perhaps it was omitted because its leaders were not involved in any colorful fracases. Also it is worthy of note that many of the state ornithological societies match the national organizations in attendance at meetings and approach them in quality of programs.

Some readers may be disappointed not to find their local or regional heroes in this book. A few may be reminded of "The New Yorker's" map of the United States, with not much west of the Hudson River but California. But it surely was not just xenophobia that caused Midwesterners in the early days to point out that Easterners in the publishing centers might have been more accurate about the ranges and habits of birds if they had been more attentive to the pages of "The Wilson Bulletin." It was Maurice Brooks of West Virginia, not quoted by Kastner, who noted that the literary skills of New Englanders had captured the public mind with provincial impressions that were not accurate elsewhere. For example, Southerners do not recognize their Yellow-breasted Chat (*Icteria virens*) in the descriptions of it as shy and elusive in most bird books. Many birds at the periphery of their ranges are quite different from their fellows in their heartlands. Michigan people are surprised to read in the classic accounts that the Hermit Thrush (*Catharus guttatus*) is the songster of the swamps, when they know it as an inhabitant of dry sandy uplands.

Many ornithologists who learned birds decades ago in the parks, cemeteries, garbage dumps, and reservoirs of cities will be astonished to learn that urban bird watching was transformed by a small group of boys in New York City. The Bronx County Bird Club looks big from Manhattan, but it was not unique for its time. Its story could be matched in a score of other cities. I am reminded of a group of distinguished scientists who in their youth at Columbus, Ohio, put Green Lawn Cemetery and Buckeye Lake on the ornithological map.

This book, as noted, is about people, and as such understandably it may credit a few prominent individuals with undue influence on the sweep of events. Whether such people created the tide or just rode with it is a difficult historical question. Certainly some of the forces that led to the "world of watchers" were scattered and obscure. An underlying factor was the rise in leisure and literacy, not only in America but around the industrialized world. Today the new urban population has awakened to nature's beauties that were often taken for granted back on the farm.

Even for specific forces, the real authors are sometimes lost in history. Who originated the Boy Scout merit badge on birds or the colored pictures distributed nationwide in boxes of Arm and Hammer baking soda? The teachers who inspired their students are legion, and they often came from colleges like Oberlin, in Ohio, which offered the first ornithological course in America. The modern field guides are great and they have helped to popularize

bird watching, but something else inspired the millions of people with backyard feeders but not guides.

This is a handsome book, with elegant typography. All the chapters begin with Louis Agassiz Fuertes field sketches, and the center of the book holds eight unnumbered color plates of Fuertes' paintings. The volume is admirably free of typographical errors, and I saw only two worthy of mention, the names of friends of mine, Oscar McKinley Bryens on p. 144 and Miklos D. F. Udvardy on p. 230.

This book is lively reading and factually accurate. It is embellished with an excellent index and complete bibliography. Everyone interested in the personalities and events leading up to the present vogue in bird watching will enjoy it.—HAROLD F. MAYFIELD.

WILDERNESS AND NATURAL AREAS IN THE EASTERN UNITED STATES: A MANAGEMENT CHALLENGE. by David L. Kulhavy and Richard N. Conner (eds.). Proceedings of the Symposium (1985), published by School of Forestry, Stephen F. Austin State Univ., Nacogdoches, Texas, 1986:416 pp. $30.00.—This attractive, hard-backed book contains 69 papers that were presented at a symposium held May 1985. The book is organized into 8 sections: "Introduction" (6 papers), "Wildlife" (14 papers), "Forest Protection" (7 papers), "Management Issues" (12 papers), "Visitor Needs and Issues" (11 papers), "Vegetation" (9 papers), "Grasslands and Savannahs" (9 papers), and "Summary" (1 paper). All papers contain a brief abstract plus a list of key words. Positive features which greatly increase the usefulness of this book are the "Taxonomic Index" (366 entries) and "Subject Index" (504 entries). The former includes the scientific names of 12 birds, most of which are mentioned in the 3 papers dealing directly with birds. These papers are: "The Effects of Wilderness on the Endangered Red-cockaded Woodpecker," "Raptors and Eastern Wilderness," and "Wilderness as Wild Turkey Habitat in the Eastern United States." Unfortunately, the index lists only those scientific names mentioned in the text narrative and not those listed in tables or figures. The "Subject Index" has 45 listings of bird names, including common names of species and scientific names of families.

A variety of topics is covered, ranging from single species and specific wilderness sites to broad issues and policies for the entire eastern United States. Line drawings and photographs (both black-and-white and color) are used judiciously to illustrate the text. Typographical and classification errors are scattered throughout, but are more annoying than misleading. For example, marten is listed in the Subject Index under birds, while prairie chicken is listed under mammals.

All major wilderness and natural areas within the eastern United States are well represented in most sections. One exception is the "Vegetation" section, in which 8 of the 9 papers involved only areas in east Texas. Eastern wilderness areas have a higher value than do western areas because of their scarcity, small size, and proximity to heavily populated eastern cities. These same attributes result in eastern wilderness areas being more difficult to manage than western ones. Thus, the discussions of management strategies and policies, which comprise a major portion of this book, will play an important role in the future of these eastern areas. This book should be consulted by anyone interested in research or management of eastern wilderness or natural areas.—E. D. MICHAEL.

THE WILD PALISADES OF THE HUDSON. By John Serrao. Lind Publications, Westwood, New Jersey, 1986:169 pp., 24 color illus., numerous black-and-white illus., maps, and tables. $28.00.—The Palisades Interstate Park of New Jersey-New York is one of the most visited natural areas in America, with more than 6 million users annually. This noteworthy area

along the Hudson River has been called the "finest, most scenic and accessible urban park in the nation," and its natural history is now well reviewed in one volume.

This attractive volume provides a detailed introduction to the geology, flora, and fauna of the Palisades, and a comprehensive guide to recreational locations (from nature centers and sanctuaries to county parks). The author has been in environmental education here for years, and is intimately familiar with the Palisades. The book's chapters include: "Geology," "Early History," "Habitats," "Flora," "Fauna," and "Convervation." The review of birdlife (about 275 species) includes summaries with data of birding areas and activities from local Christmas counts, breeding bird censuses, autumn hawk counts (Hook Mountain), and the like. Serrao himself has made a study of the decline in migrant woodland birds breeding here (dramatic population reductions of the neotropical migrants since the 1950s). For all such topics there is a thorough bibliography and list of readings.

The second half of the book is a guide, with specific site descriptions and comments on the natural history highlights (e.g., a rocky cliff for skinks, etc.). For many of the sites detailed trail maps are included, and some of the areas have a long ornithological history such as Piermont Marsh and Hook Mountain.—CHARLES F. LECK.

BIRDS: A GUIDE TO THE LITERATURE. By Melanie Ann Miller. Garland, New York, New York, 1986:887 pp. $100.00.—This book was written to facilitate accessibility to information on birds and to promote wildlife conservation and environmental awareness of the general public. There are 1942 citations. well annotated with a description of the book, its coverage, list of key words and phrases, illustrations, and additional features such as bibliographies, species lists, and historical information. Most of the recent major domestic and foreign books are included, up to about 1983. The coverage of books published prior to the 1950s seems uneven. The citations are arranged in the following categories (number of citations in each follows in parentheses): "Guide to general works": "Dictionaries, encyclopedias and glossaries" [17], "Bibliographies, catalogs and indexes" (8); "Guide to subjects" (625), with 16 subheadings, including "Art," "Behavior," "Classification," "Evolution," "Song," and others; "Species and group studies" (343), arranged alphabetically by the species or group name as it appears in the title of the book; "Area studies" (539), alphabetically by geographic regions, continents, countries, and states; "Field guides" (90), arranged as in previous sections; "Children's literature" (296), arranged under same subheadings as in "Guide to subjects"; "Biographies" (14), alphabetically; and "Fiction" (5). An Appendix follows, listing 50 journals and periodicals, and the names and addresses of the organizations that publish them. Last, and unfortunately least, is the Index. There is no listing of the subheadings used, except under the "Subject" heading.

The author is not an ornithologist, and appears to be unfamiliar with the literature; some valuable and standard books are omitted. For example, under Kirtland's Warbler (*Dendroica kirtlandii*), the only listing is for "Kirtland's Warbler," (Walkinshaw, 1983), while Mayfield's (1960) excellent "The Kirtland's Warbler" and Huber's (1982) comprehensive "The Kirtland's Warbler (*Dendroica kirtlandii*): An Annotated Bibliography 1852–1980" are not included. Under Peru, "Bird Islands of Peru." (Murphy 1925) and "An Annotated Checklist of Peruvian Birds" (Parker et al. 1982) are listed, while "The Birds of the Dept. of Lima, Peru" (Koepcke 1970) and "Gazetteer of Peru" (Stephens and Traylor 1983) are not. The Biographies section is very limited.

The author's lack of knowledge of taxonomy causes some problems: North American blackbirds and the European blackbird are listed together, while the American Robin (*Turdus migratorius*) and European Robin (*Erithacus rubecula*) are separated. From the annotations

one cannot always tell which species groups are included, and many species actually covered are not listed: chickadee, turkey, and nighthawk, for example.

Access to the citations contained in the book is rather difficult. There is very little cross-referencing from one heading or subheading to another. This is especially apparent in the species listings, where cross-referencing would have been very useful for the layman. Each book is found under the name of the particular group or species as it appears in the title, not grouped taxonomically. Thus, a student interested in reading about waterfowl would find books listed under the following subheadings: "Black Brant," "Black Duck," "Blue-winged Teal," "Canada Goose," "Canvasback," "Ducks," "Geese," "Giant Canada Goose," "Greylag Goose," "Hawaiian Goose," "Mallard," "Shelduck," "Pinkfoot Goose," "Snow Goose," "Swans," "Trumpeter Swan," "Water birds," "Waterfowl," "Whistling Swan," and "Wild Fowl." No student would know to look under all of these, and there is no way to find these headings other than paging through the entire Species section of 152 pages. Either the books should have been grouped under taxonomic headings, or purely alphabetically with a decent title and subject index provided. This is not so much of a problem in the other sections, which are generally shorter, or arranged alphabetically by geographic region.

The Index consists almost entirely of a listing of authors with a few general texts by title. The addition of title, subject, and general taxonomic headings in the index would have made this book a valuable bibliographic tool, and worth its price. As it is, this is a good collection of references, but the average student or public librarian will not have access to them.

It seems a shame that Ms. Miller took the considerable time and effort to produce a book which she genuinely hoped would promote the public's access to and awareness of ornithological literature, and yet because of the lack of an adequate index instead provides only incomplete access and a frustrating experience for the user.—JANET G. HINSHAW.

BEYOND BIRDING. By Thomas C. Grubb, Jr. Boxwood Press, Pacific Grove, California, 1986:195 pp., 16 numbered figs., 67 tables, numerous in-text sketches. $9.95.—In North America at least, birdwatching is more sport than science. But although many of us have bemoaned this fact for some time, few of us have attempted to do anything about it. "Beyond birding" attempts to right this wrong by bringing "the basics of analytical ornithology and scientific method within the reach and interest of the amateur student of birds." The book, which is not so much an introductory text as it is a compilation of field exercises, includes 2 introductory chapters (one on ornithology as a science and another on "analytical [i.e., hypothetico-deductive] ornithology"), 20 chapters that described projects in analytical ornithology, a concluding chapter entitled "What to do when you know this book," 2 appendixes on statistical analysis, and one that lists the scientific names of birds mentioned in the text. Although both the book's title and its "how to" format indicate that the intended readers of the text are independent amateur birders, many of the projects outlined in the book are probably more appropriate for students enrolled in high-school and college level courses in biology.

The heart of the book is its 20 "project" chapters, each of which begins with a question (e.g., Why do Osprey [*Pandion haliaetus*] hover? Can Turkey Vultures [*Cathartes aura*] smell their way to food? Can birds divide energy by seconds?), which Grubb challenges the reader to answer using the scientific method. Although all of the projects appear doable—it is unclear that all were field tested—some will be considerably easier to carry out than others. None requires capturing birds. Most of the projects fall within the confines of mainstream behavioral ecology, most deal with foraging behavior, and most can be accomplished in a few days to several weeks. All of the chapters include suggestions for statistical analysis of the data. Only one of the projects is directed at a "long-term" question (Do populations

of Black-capped [*Parus atricapillus*] and Carolina [*P. carolinensis*] chickadees ebb and flow?). Given the value and necessity of such studies (e.g., Likens, Bull. Ecol. Soc. Am. 64:234–243, 1983), and the proved ability of amateur ornithologists to collect these kinds of data, it is unfortunate that a greater portion of the text is not devoted to such studies.

The introductory chapters are fine as far as they go, but I suspect these brief (<12 pages of 5½ × 8½ text), telegraphic outlines of hypothetico-deductive reasoning and both descriptive *and* analytical statistics will prove too challenging for the amateur ornithologist, especially with regard to the statistics. (It seems a pity that so many excellent birders are afraid of numbers—except, of course, those in their life lists.) High-school and college students, however, are another group entirely, and I suspect the book will be fertile ground for those in search of science-fair projects and subjects for term papers. "Beyond Birding" will also be useful to those of us who teach college ornithology and are in need of ideas for field "labs."

Grubb's effort is a laudable one, but it only begins to fill a niche that has been vacant far too long. I hope it finds itself in competition soon.—K.L.B.

THE 1984 FIELD ORNITHOLOGY INDEX. By John Kennington (ed.). Puffin Publications, Box 581862, Tulsa, Oklahoma 74158, 1986:v + 126 pp. $22.00.—The task of keeping up with the expanding literature of ornithology is a difficult one, and this book represents a modest attempt to make the job easier. It is subtitled "A key word index to journals referencing North American birding and field ornithology." The heart of the system is the "Kwic Index" in which titles are arranged alphabetically by key words, including species, location, and general subject. On finding the title of interest, one consults a code designation that leads one to the proper citation in the Bibliography list. The procedure worked very well for the several test topics I tried to find.

An appendix lists the 48 journals, including three non-North American ones, whose papers are indexed. The majority are state publications but several of these are not included. The subtitle accurately defines the limits of coverage.This "index" covers the literature for 1984, and 1985 and 1986 are promised for delivery by May 1987, with annual publication in May thereafter.—GEORGE A. HALL.

PROCEEDINGS OF HAWK MIGRATION CONFERENCE IV. By Michael Harwood (ed.). Hawk Migration Association of North America, 1986:xi + 393 pp., many black-and-white maps and figs. $29.95. (Obtainable from: HMANA, % Richard Morton, 604 Windsor Place, Moorestown, New Jersey 08057.)—At hand is a collection of 33 papers delivered in 1983 at Rochester, New York, at the Fourth Hawk Migration Conference. The monitoring of the raptor migrations, particularly in the autumn, has attracted the efforts of many amateur, as well as professional ornithologists, and the Hawk Migration Association of North America (HMANA) has been very successful in coordinating much of this effort. Eighteen of these papers are descriptions of events at specific sites, some summarizing several years of activities but others giving data for only a single year. Eight of the papers deal with techniques of analyzing the data or improving the collection of them. Five papers give reviews of broad topics and 7 might be called theoretical papers. As is usual with symposium collections the quality and interest of the papers is highly variable, and a reader might wish some of the theoretical papers were longer and more detailed. Dedicated hawk watchers will consider this a "must" book, and other students of migration will find much of interest.—GEORGE A. HALL.

EIDER DUCKS IN CANADA. By Austin Reed (ed.). Canadian Wildlife Service Report Series No. 47, Ottawa, Canada, 1986:177 pp., many black-and-white photos and maps. $19.50 (Canadian) in Canada, $23.40 in other countries.—This is a collection of 18 papers detailing all aspects of the biology and management of the Common Eider (*Somateria mollissima*). The papers are grouped under the headings: "Distribution and Abundance"; "Races of the Common Eider"; "Distribution in Winter"; "Ecology"; "Use by People"; and "Conclusions." Twelve of the papers are in English, and 5 are in French, with the final paper in both languages. Each paper has an abstract in the other language and those papers of special interest to the Inuit (11) have abstracts in Inuktitut.—GEORGE A. HALL.

Wilson Bull., 99(4), 1987, pp. 748–758

PROCEEDINGS OF THE SIXTY-EIGHTH ANNUAL MEETING

JOHN L. ZIMMERMAN, SECRETARY

The Sixty-eighth Annual Meeting of the Wilson Ornithological Society was held Thursday, 28 May to Sunday, 31 May 1986 at Utica College of Syracuse University, Utica, New York in joint session with the Eastern Bird Banding Association. In addition to Utica College, the meetings were sponsored by the Kirkland Bird Club and the Oneida Bird Club. Dr. Judith W. McIntyre chaired the Local Committee on Arrangements composed of Howard Berg, Patty Burchard, Lona Coates, Lorraine Diehl, Jim and Ginny Francis, Bill Gotwald, Fran Hanes, Dave Hazelden, Robert Hurd, Ken Karwowski, Betty Kerwin, Ferne Merrill, Pat McIntyre, Mike MacMahon, Helen Western, and Helene Whittaker.

The Council met from 13:00 to 18:30 on Thursday. Registration for the 154 guests and members began that afternoon and was followed by an evening reception in the Gannett Memorial Library Concourse. The opening session was held in Macfarlane Auditorium in DePerno Hall where the societies were welcomed by the Dean of the College, Dr. Tom Harblin. President Clait Braun responded for the Wilson Society, and Don Schwab, First Vice-President, accepted the welcome for the Eastern Bird Banding Association. The scientific papers presentations were made on Friday and Saturday, with a double session necessary on the afternoon of the first day.

Early morning field trips were scheduled both Friday and Saturday to Utica Marsh and to one of the city parks on Saturday with able leadership provided by the local committee. A spouse-guest tour to Lake Julia and the Oneida Community took place on Friday, and a mushroom exploration was held on Saturday morning. On Sunday, more extensive field trips were conducted to Verona Beach State Park, Rome Sand Plains, and the Jenny Lake banding station. An exhibit, Birds in Art, and a reception were enjoyed by all at the Munson-Williams-Proctor Institute Friday evening. Additionally, an exhibit of some of the bird paintings of Karen Allaben-Confer was available throughout the meeting at the Barrett Art Gallery, just adjacent to library concourse, and the work of Utica College's artist-in-residence, Henry DeSpirto, was on display at the Strebel Micro Gallery on the campus.

The annual banquet was held in the Strebel Student Center on Saturday evening. The following awards were presented:

EDWARDS PRIZE (for the best major article in volume 98 of *The Wilson Bulletin*)

John S. Warriner, Jane C. Warriner, Gary W. Page, and Lynne E. Stenzel, "Mating systems and reproductive success of a small population of polygamous Snowy Plovers," Wilson Bull. 98:15–37.

LOUIS AGASSIZ FUERTES AWARD

Scott R. Freeman, "A molecular phylogeny of the Icterinae."

PAUL A. STEWART AWARDS

Toni L. De Santo, "Physiological and ecological factors influencing prey selection in the White Ibis."

Peter O. Dunn, "Male parental investment, female philopatry, and the mating of Tree Swallows."
Scott R. Freeman, "The average age of adult passerines."
Dale E. Gawlik, "A field study of the distribution, abundance, and reproductive success of the Loggerhead Shrike in South Carolina."
Rogier C. Gruys, "Mortality of a wintering ptarmigan population."
Malcolm F. Hodges, Jr., "Foraging ecology of the Belted Kingfisher."
Fred L. Mikesell, "Avian habitat selection in the attenuated riparian forest on the tallgrass prairie."
Hannah B. Suthers, "Pesticide residues and death in backyard songbirds."
Teresa M. Telecky, "Roost attendance during the breeding season of the Common Myna."
Robert J. Welch, "Habitat utilization and behavior of the Red-shouldered Hawk in Wisconsin."

MARGARET MORSE NICE AWARD

L. Scott Johnson, "Singing strategies and rates of polygyny in House Wrens nesting in natural cavities."

ALEXANDER WILSON PRIZE (for best student paper at the meeting; selection committee members—Richard Banks, Mary Clench, and Helmut Mueller) shared by

Dale E. Gawlik, Winthrop College, South Carolina, "Nesting success and breeding habitat of the Loggerhead Shrike (*Lanius ludovicianus*) in South Carolina."
John A. Smallwood, The Ohio State University, "A mechanism of sexual segregation by habitat in American Kestrels (*Falco spaverius*) wintering in southcentral Florida."

FIRST BUSINESS MEETING

The first business meeting was called to order by President Braun at 08:55, Friday, 29 May in Macfarlane Auditorium. Secretary Zimmerman summarized the highlights of Thursday's Council meeting, reporting that Dr. Charles R. Blem had been elected as the new editor of *The Wilson Bulletin,* effective 1988. He also was pleased to report that the healthy financial status of the Society will not necessitate a dues increase for the coming year, but that an increase may come to pass in the following year. Lastly, Zimmerman asked those attending to stand to honor those members who had died since we last met together—Joseph L. Bell (Rocky Point, NY), Donald L. Bleitz (Los Angeles, CA), John Davis (Carmel, CA), S. Charles Kendeigh (Champaign, IL), John A. Maclean, Jr. (Winnetka, IL), Paul J. Nowland (Greenville, DE), Hollis T. Ross (Lewisburg, PA), Lucy Sierkierski (Columbus, OH), George J. Wallace (East Lansing, MI), and Joel C. Welty (Beloit, WI).

A. S. Gaunt, Chairperson of the Nominating Committee, offered the following slate for consideration by the membership: President—Mary Clench, First Vice-President—Jon Barlow, Second Vice-President—Richard Banks, Secretary—John Zimmerman, Treasurer—Robert Burns, Elected Council Member for 1988–1990—Peter Hicklin.

Robert D. Burns gave the treasurer's report.

REPORT OF THE TREASURER
1 January 1986 to 31 December 1986

GENERAL FUNDS

RECEIPTS		
Dues collected in 1986		
Regular and Sustaining Memberships for 1986	$ 11,698.00	
Regular and Sustaining Memberships for 1987	16,729.00	
Student Memberships for 1986	1,424.00	
Student Memberships for 1987	1,180.00	
Family Memberships for 1986	200.00	
Family Memberships for 1987	340.00	
TOTAL DUES		$ 31,571.00
Subscriptions to *The Wilson Bulletin*		
For 1986	$ 8,157.50	
For 1987	12,983.00	
TOTAL SUBSCRIPTIONS		$ 21,140.50
Back issues of *The Wilson Bulletin*		$ 2,033.70
Interest and Dividends		$ 21,292.84
Royalties		$ 1,937.77
Contributions from Authors		$ 5,877.30
Contributions to The Van Tyne Library		$ 147.00
Contributions to the Student Membership Endowment		$ 399.00
Contributions to General Endowment (Life Members and Patrons)		$ 3,084.00
Contributions to the Edwards Prize		$ 350.00
Contributions to the Wilson Prize Endowment		$ 290.00
Contributions to the Centennial Fund		$ 1,629.00
Surplus funds from the Annual Meeting		$ 1,650.00
TOTAL RECEIPTS		$ 91,402.11
DISBURSEMENTS		
The Wilson Bulletin		
December 1985	$ 17,262.12	
March 1986	15,402.71	
June 1986	12,734.04	
September 1986	13,757.01	
Editorial Expenses	3,618.86	
Colorplates	2,507.54	
TOTAL PRODUCTION COSTS		$ 65,282.28
OSNA Expenses		$ 8,100.00
Student Awards		$ 2,950.00
Treasurer's Expenses		$ 351.00
Mailings, Student Membership Award Notices		$ 83.85
ICBP Dues		$ 100.00
Subscriptions and OSNA Refunds		$ 2,674.75
Printing and Mailing of Back Issues		$ 200.00
Incorporation Fee		$ 5.00
Bank Charges		$ 6.47
TOTAL DISBURSEMENTS—1 January 1986 to 31 December 1986		$ 79,753.35
1985 DEFICIT		$ 6,503.99

ENDOWMENT FUNDS

Color Plate	$ 29,652.46
Wilson Prize	1,863.09
Fuertes/Nice Awards	10,120.00
Stewart Awards	23,194.75
Edwards Prize	1,393.94
Student Member	910.11
General Endowment	167,243.45

The Editor's report was presented by Keith L. Bildstein.

EDITOR'S REPORT—1986

In 1986 186 manuscripts (66 papers, 120 communications) were submitted to my office. This is an 11% increase over the number of manuscripts submitted in 1985. Of these, 48% have been accepted, 42% have been rejected, 1% have been withdrawn, 8% have been returned to authors for revision, and 1% are still under review. Based on these figures, I project acceptance rates of 55% for manuscripts submitted as major papers and 50% for manuscripts submitted as short communications. Manuscripts accepted for publication are usually published within 5–9 months of acceptance. Major papers received in 1986 were returned to the author within 85 ± 43 days of receipt. Short Communications received in 1986 were returned within 72 ± 48 days of receipt.

Over the past year I have received essential assistance from many people in the Editorial Office and elsewhere. I thank the staff of the Allen Press, especially Arly Allen, Ken Blair, John Breithaupt, Guy Dresser, and Sharon Kindall. Others that I thank for their outstanding service include: Associate Editors M. W. Collopy, R. N. Conner, J. P. Myers, W. M. Shields, and J. R. Walters; Assistant Editors A. E. Conway, J. A. Hovis, J. W. Johnston, J. B. Olson, D. L. Rankin, D. Gawlik, and A. Wenner; Review Editor George A. Hall; Color Plate Editor W. A. Lunk; Index Editor K. G. Beal; numerous members of the WOS, including C. Braun, S. Gaunt, A. Gaunt, J. Barlow, J. Jackson, and B. Burns; the 190 volunteer referees who reviewed manuscripts for the *Bulletin* during the past 11 months; and Department of Biology secretaries A. Jones and S. Strait.

I view my pending retirement as Editor with mixed emotions. My successor faces the challenges of a Centennial Year replete with numerous special considerations. He also faces a continually changing readership and authorship. Most importantly, he faces the thrill and excitement of editing, something that will most certainly speed his ornithological education, if not his aging process. Editing *The Wilson Bulletin* has been both gratifying and humbling. The responsibility has been enormous, but so has the opportunity to advance my education. I know considerably more now—both about writing and about science—and I hope that evidence of my knowledge has been transmitted through the pages of *The Wilson Bulletin.*

Keith L. Bildstein, *Editor*

Stan Senner, representing the local committee on arrangements for the centennial meeting, reported that the meeting will be held at Rosemont College in suburban Philadelphia on 8–12 June 1988.

SECOND BUSINESS MEETING

President Braun reconvened the Society for the second business meeting at 13:02 in Macfarlane Auditorium on Saturday, 30 May. The report of the auditing committee was received. Chairperson Zernickow presented the report:

We, the undersigned, have reviewed the financial records presented by the Treasurer, covering the period of 1 January 1986 to 31 December 1986, with the intent of verifying that the records correctly reflect the assets and liabilities of the Society, and the correct and timely posting of income and expenditures during this period. We found no errors or omissions and are satisfied that the financial reports covering operational activities and the various endowment funds are correct. We commend Dr. Robert Burns, treasurer, for his excellent performance in fulfilling the responsibilities of his office for the year 1986, and for taking the initiative to computerize the records on his personal computer.

Herbert P. Zernickow, *Chairman*
Robert A. Whiting
William A. Klamm

A motion to accept the report of the Auditing Committee was made by Richard Stiehl, seconded by Jerry Jackson, and passed by the membership.

The Report of the Nominating Committee was recalled to the floor by President Braun and opened for further nominations. In the absence of additional nominees, it was moved by Dick Scott and seconded by Jerry Jackson to close the nominations and accept the slate as presented by the Nominating Committee. With the passage of this motion it then was moved by A. S. Gaunt to elect the slate by acclamation. With a second by Herbert Hendrickson, the motion was passed.

A list of the 153 new members of the Society had been posted at the meeting. Ken Parkes moved and Helen Lapham seconded to accept these new members of the Wilson Ornithological Society. The motion passed.

Richard Stiehl presented the report of the Resolutions Committee.

REPORT OF THE RESOLUTIONS COMMITTEE

WHEREAS, the Wilson Ornithological Society has met for the first time with the Eastern Bird Banding Association, and

WHEREAS, the interactions on both social and professional levels were wholeheartedly enjoyed by the members present at Utica College of Syracuse University,

THEREFORE BE IT RESOLVED that sincere and concerted efforts be made to hold additional meetings and that indeed a tradition of joint meetings of the societies be established.

Mary Clench moved and Doug James seconded to accept this resolution. The motion passed.

WHEREAS, Keith L. Bildstein has ably served as Editor of *The Wilson Bulletin* since 1984, and

WHEREAS, he, in this time of service, has maintained and extended the highest standards of excellence in *The Wilson Bulletin*, and

WHEREAS, Dr. Bildstein has simultaneously guided the production of the *Bulletin* with excellent promptness,

THEREFORE BE IT RESOLVED that the membership of the Wilson Ornithological Society at their 68th Annual Meeting at Utica College of Syracuse University extend their sincere appreciation and thanks to Keith L. Bildstein for the excellence of performance during his tenure as Editor of *The Wilson Bulletin*. We wish you well.

It was moved by Judy McIntyre and seconded by Jeff Spendelow to accept this resolution. The motion passed.

WHEREAS, the Wilson Ornithological Society, along with the Eastern Bird Banding Association, have held their joint meeting in pleasant surroundings at Utica College of Syracuse University in New York, and

WHEREAS, the Kirkland Bird Club and the Oneida Bird Club as co-sponsors have jointly been responsible for our relaxed and enjoyable time, and

WHEREAS, the Local Committee on Arrangements, ably chaired by Judith W. McIntyre, has labored long and diligently to assure the success of this first joint meeting of these two societies, and

WHEREAS, balmy weather conditions, a stimulating scientific program, the many opportunities for observations of local birds, the esthetically rewarding presentations of artworks, as well as an introduction to some of the finer wines and beers of New York State all contributed to make this a memorable and superbly organized gathering,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society commends the sponsoring groups and salutes the Local Committee on Arrangements for a job well done.

The motion to accept this resolution was made by Kathleen Klimkiewicz, seconded by Richard Banks, and passed by the membership.

A motion for adjournment was made by George Hall and seconded by Helmut Mueller. Before adjourning, however, the assembled membership gave a standing round of applause to the outgoing President, Clait Braun, for a job well done.

The reports of the standing committees were given as follows:

REPORT OF THE COMMITTEE ON STUDENT MEMBERSHIP—1986

A total of 215 letters was sent to Wilson Ornithological Society members with positions at academic institutions asking that they encourage students to apply for a student membership award. Only 6 completed applications were received, although the names of 4 other potential student members were forwarded by one member. Six students are recommended for student membership awards to be given in 1987. They are John M. Bates—University of Arizona, Arlene K. Blumton—Virginia Polytechnic Institute, Mark D. Dixon—Iowa State University, Daniel Esler—Texas A&M University, David A. Haukos—Texas Tech University, and John Kusnier, Jr.—University of Toledo.

Student Membership Awards in the Wilson Ornithological Society were initiated when Mrs. A. M. Bagg donated money to the Society in 1973–74 for this purpose in memory of her husband, President of WOS in 1966–68. The first awards were given in 1975 and were called the Aaron M. Bagg Student Membership Awards. They retained this name through 1982, and became known as Student Membership Awards funded by WOS Council in 1983. From 1975 through 1983, a total of 176 awards was given of which 92 (52%) of the recipients were still members of WOS in 1985.

Different methods have been used to solicit applications for Student Membership Awards, ranging from large mailings (200 to 850 letters/year) to printing announcements of the awards in the *Ornithological Newsletter* and *The Wilson Bulletin*. No one method has been more effective than another. Council is encouraged to reconsider the thrust and need for continuation of Student Membership Awards.

Clait E. Braun, *Acting Chairperson*

MEMBERSHIP COMMITTEE REPORT—1986

A new updated membership brochure (blue) was printed in early 1986 and quantities were sent to key people within the WOS Council. In addition, letters and copies of the

brochure were sent to over 200 WOS members who had academic positions for the purpose of making them available to interested faculty, staff, and students. Almost no feedback was received regarding this effort, although less than 5 requests for more brochures were received. Additionally, 3 WOS members were asked to chair the WOS Membership Committee with restructured priorities (especially concentrating on state ornithological groups). The chair of this committee was not filled. Council should reconsider the need for and thrust of the Membership Committee.

Clait E. Braun, *Acting Chairperson*

LIBRARY COMMITTEE REPORT—1986

During the year 1986, the Josselyn Van Tyne Library activities continued much as usual, without any particular fanfare but with results at the levels we have come to expect: some modest increases and a few slight drops, in the summary figures. Once again, let us be thankful that Janet Hinshaw can manage along with her many duties to keep our affairs organized and pretty well up to date. The committee itself having remained unchanged for a number of years, we are pleased with the appointment of Mary McKitrick (newly arrived at U. of M.) as an additional member.

The promised publication, "A Bibliography of Ornithological Translations," by D. Siegel-Causey and Janet Hinshaw, has now appeared in *Current Ornithology,* vol. 4. It includes the considerable collection of translations available in our library.

From a total of 31 generous members came 1237 donated items, including 65 books, 850 journal issues, 246 reprints, 11 theses or dissertations, 62 reports, 1 translation, and 1 computer program. The donors were: G. F. Barrowclough, R. D. Bayer, A. J. Berger, R. B. Clapp, C. T. Collins, W. N. Davey, S. M. Doehlert, J. Gapzynski, L. Garret (for Patuxent W. R. C. Library), S. M. Goodman, G. A. Hall (for *Wilson Bulletin* review copies), K. W. Haller, P. Hamel, J. G. Hinshaw, S. Holohan, M. Kynast (for Univ. Detroit Library), H. Lapham, F. E. Lohrer, K. Meyer, E. H. Miller, S. B. McNair, R. B. Payne, T. H. Pogson, R. L. Phillips, W. V. Reid, W. R. Solomon, R. W. Storer, W. and C. Taylor, W. Thiede, and L. R. Wolfe.

Although the swelling list is gratifying, we should urge even more members to contribute. Items that do not find their way directly to our shelves can be just as valuable through sales to support the New Book Fund.

This year, the above mentioned fund took in $350.50 from the sale of 25 duplicate books and 69 journal issues. For $220.30 we purchased books, records, indices, reports, etc., totaling 28 items.

The library received 210 journals and other items: 159 titles from 117 direct exchanges, 40 titles from 29 gifts, and 11 titles from 7 subscriptions.

Best of all, our list of loans keeps gradually growing—and this is, after all, where the membership reaps its most direct benefits. In 82 transactions, loans of 291 journals, books, and photocopies went to 47 individuals.

The committee thanks everyone who has helped, and urges an ever-broadening base of support.

William A. Lunk, *Chairperson*

CONSERVATION COMMITTEE REPORT—1986

This year's report is presented as two papers submitted for publication to *The Wilson Bulletin*: "Conservation of North American Rallids" by William R. Eddleman, Fritz L.

Knopf, Brooke Meanley, Frederic A. Reid, and Richard Zembal, and "Conservation of riparian ecosystems in the United States" by Fritz L. Knopf, R. Roy Johnson, Terrell Rich, Fred B. Samson, and Robert C. Szaro.

The Committee on Scientific Program (Jon C. Barlow, Chair, Heather Ardies, and Elsa Melynchuk) with the help of session moderators John Zimmerman, Dick Banks, Doug James, George Hall, Dick Stiehl, Mary Clench, Richard Conner, Jerry Jackson, and A. S. Gaunt offered the following program:

PAPER SESSIONS

L. L. Short, Dept. Ornithology, American Museum of Natural History, New York, NY; J. F. M. Horne, National Museum Kenya, Nairobi, Kenya; and J. A. Jackson, Dept. Biological Sciences, Mississippi State Univ., Mississippi State, MS, "The current status of the Ivory-billed Woodpecker in Cuba."

J. C. Barlow and M. K. Peck, Dept. Ornithology, Royal Ontario Museum, Toronto, ONT, "Status of two Caribbean scrub vireos."

W. H. Knight, Dept. Zoology, Univ. Toronto, Toronto, ONT, "Patterns of endemism in the birds of Wallacea."

J. W. Hardy, Florida State Museum, Gainesville, FL, "New nightjar sound recordings and their bearing on *Caprimulgus saturatus* and *C. sericocaudatus*."

R. C. Banks, U.S. Fish and Wildlife Service, National Museum of Natural History, Washington, DC, "Geographic variation in the Yellow-billed Cuckoo (*Coccyzus americanus*)."

J. D. Webster, Hanover College, Hanover, IN, "Skeletal characters and the genera of warblers."

D. F. Stotz, Committee on Evolutionary Biology, Univ. Chicago, Chicago, IL, "Phenotypic correlation patterns in Swamp Sparrow (*Melospiza georgiana*) flight feathers."

D. S. Wood, Carnegie Museum of Natural History, Pittsburgh, PA, "The occurrence and use of collections of spread wings."

N. S. Mueller, Dept. Biology, North Carolina Central Univ., Durham, NC, "Experimental study of neonatal tolerance in Mallard ducklings (*Anas platyrhynchos*)."

N. Sabine, Dept. Zoology, Brigham Young Univ., Provo, UT, "Do communal roosts serve as information centers for Bald Eagles?"

D. James, J. Fitzgerald, and C. Riley, Dept. Zoology, Univ. Arkansas, Fayetteville, AR, "Relationships between population levels of wintering Bald Eagles and other raptors in northwestern Arkansas."

H. C. Mueller, Dept. Biology, Univ. North Carolina, Chapel Hill, NC, "Fall migrations of Cooper's Hawks (*Accipiter cooperii*) at Cedar Grove, WI, 1936–86."

D. Klem, Jr., Dept. Biology, Muhlenberg College, Allentown, PA; S. E. Senner and L. H. Goodrich, Hawk Mountain Sanctuary Association, Kempton, PA, "Trends in numbers of migrating raptors at Hawk Mountain Sanctuary from 1934 to 1986."

C. R. Chandler, Dept. Biology, Bowling Green State Univ., Bowling Green, OH; and R. S. Mulvihill, Carnegie Museum of Natural History, Pittsburgh, PA, "Wing shape variation in the Dark-eyed Junco (*Junco hyemalis*)."

K. E. Parker and R. L. Miller, Wildlife Resources Center, Delmar, NY, "Status of New York's Common Loon population—comparison of two intensive surveys."

J. A. Spendelow, U.S. Fish and Wildlife Service, Patuxent Research Center, Laurel, MD, "Population dynamics of Roseate Terns in Connecticut: modeling annual survivorship using capture-recapture models."

S. Droege and J. R. Sauer, U.S. Fish and Wildlife Service, Laurel, MD, "Changes in abundance of selected North American breeding bird populations over the past 20 years."

D. A. Gross, Susquehanna Biology Lab., Berwick, PA, "Relatively stable or increasing breeding bird populations in two Pennsylvania forest plots."

E. K. Bollinger, T. A. Gavin, and D. C. McIntyre, Dept. Natural Resources, Cornell Univ., Ithaca, NY, "Comparison of line transect and variable circular-plot methods for estimating Bobolink (*Dolichonyx oryzivorus*) densities."

R. T. Engstrom and G. S. Butcher, Cornell Laboratory of Ornithology, Ithaca, NY, "Using colonial bird register data to monitor population trends in the Least Tern (*Sterna antillarum*)."

R. S. Mulvihill, D. S. Wood, and R. C. Leberman, Carnegie Museum of Natural History, Pittsburgh, PA, "Seasonal variation in the sex ratio of Ruby-throated Hummingbirds."

S. Wiles-Ehmann and W. M. Shields, College of Environmental Science and Forestry, SUNY, Syracuse, NY, "Mixed reproductive strategy in the Barn Swallows (*Hirundo rustica*)."

B. D. Watts, Dept, Biology, College of William and Mary, Williamsburg, VA, "Parental defense decisions: as evidenced by temporal trends in predator-related clutch mortality."

Beatriz Torres, Dept. Zoology, The Ohio State Univ., Columbus, OH, "Why do Hoatzins copulate so much?"

R. W. Dexter, Dept. Biological Sciences, Kent State Univ., Kent, OH, "Incompatibility and nesting failure in a breeding colony of Chimney Swifts (*Chaetura pelagica*)."

B. Whitmar, II, Dept. Biology, Southeast Missouri State Univ., Cape Girardeau, MO, "Quantification of nesting site components in the Mississippi Kite (*Ictinia mississippiensis*)."

D. E. Gawlik, Dept. Biology, Winthrop College, Rock Hill, SC, "Nesting success and breeding habitat of the Loggerhead Shrike (*Lanius ludovicianus*)."

G. H. Farley, Div. Biology, Kansas State Univ., Manhattan, KS, "Comparative breeding habitat selection of two coexisting passerines: Bell's Vireo (*Vireo bellii*) and Bewick's Wren (*Thryomanes bewickii*)."

J. A. Sedgwick and F. L. Knopf, U.S. Fish and Wildlife Service, National Ecology Center, Ft. Collins, CO, "Habitat relationships of cavity-nesting birds in plains cottonwood bottomlands."

J. L. Confer, C. A. Braun, and M. M. Jackson, Biology Dept., Ithaca College, Ithaca, NY, "Downy Woodpecker (*Picoides pubescens*) foraging strategies: predation on insects in goldenrod galls."

M. S. Woodrey and T. A. Waite, Dept. Zoology, The Ohio State Univ., Columbus, OH, "Diurnal rhythms in caching rate and body mass in White-breasted Nuthatches: trade-off between the risks of starvation and predation?"

K. C. Parkes, Carnegie Museum of Natural History, Pittsburgh, PA, "Was the Socorro Mockingbird (*Mimodes graysoni*) a predator on small birds?"

M. Brittingham, Dept. Wildlife Ecology, Univ. Wisconsin, Madison, WI, "Does winter bird-feeding promote dependency?"

D. K. Dawson, J. R. Sauer, and J. K. Klimkiewicz, U.S. Fish and Wildlife Service, Laurel, MD, "Body mass and fat score dynamics in relation to weather in seven winter resident bird species in Maryland."

M. Clench and J. R. Mathias, Univ. Virginia, Charlottesville, VA, "The cecum: an environmentally responsive, multipurpose organ."

K. E. Parker, Wildlife Resources Center, Delmar, NY, "Common Loon reproduction on acidified lakes in Adirondack Park, New York."

B. Sample, Dept. Entomology & Applied Ecology, Univ. Delaware, Newark, DE, "Effects of a single oral dose of carbaryl on nestling Wood Thrush."

H. B. Suthers, Dept. Biology, Princeton Univ., Princeton, NJ, "Pesticide residues and death in backyard songbirds."

R. N. Conner, Southern Forest Experiment Station, USDA Forest Service, Nacogdoches, TX, "2,4-D injection to remove hardwood midstory within Red-cockaded Woodpecker (*Picoides borealis*) colonies."

J. N. Page, Dept. Environmental Conservation, Region 6, Utica, NY, "Habitats and their fauna, two state wetland acquisitions in Oneida and Herkimer counties, New York."

B. L. Swift, Dept. Environmental Conservation, Delmar, NY, "Avian breeding habitats in Hudson River tidal marshes."

D. C. Morimoto, Biology Dept., Boston Univ., Boston, MA, "Habitat relationships of birds in southeastern Massachusetts pine barrens."

J. L. Confer and M. H. Frech, Biology Dept., Ithaca College, Ithaca, NY, "The Golden-winged Warbler (*Vermivora chrysoptera*) in New York: changes in range, abundance and habitat use."

K. J. Schneider, New York Natural Heritage Program, Wildlife Resources Center, Delmar, NY, "Heritage Programs: making conservation good science."

A. Burchsted, Dept. Biology, College of Staten Island, Staten Island, NY, "Winter territories of Yellow-rumped Warblers (*Dendroica coronata*) associated with Yellow-bellied Sapsucker (*Sphyrapicus varius*) feeding trees."

J. A. Smallwood, Dept. Zoology, The Ohio State Univ., Columbus, OH, "A mechanism of sexual segregation by habitat in American Kestrels (*Falco sparverius*) wintering in south-central Florida."

M. A. Graham, Dept. Fishery and Wildlife Biology, Colorado State Univ., Ft. Collins, CO; and C. E. Braun, Colorado Div. Wildlife, Ft. Collins, CO, "Changes in territory size of White-tailed Ptarmigan."

ATTENDANCE

ARKANSAS: *Fayetteville,* Douglas James.

COLORADO: *Fort Collins,* Clait Braun, James Sedgwick.

CONNECTICUT: *Guilford,* Fred C. Sibley, Margaret Sibley; *Manchester,* Paul Lescault.

DELAWARE: *Newark,* Bradley Sample.

DISTRICT OF COLUMBIA: *Washington,* Richard Banks.

FLORIDA: *Gainesville,* J. William Hardy; *Lehigh Acres,* Ben Kiff, Maxine Kiff.

ILLINOIS: *Chicago,* Douglas Stotz; *Charleston,* L. Barrie Hunt, Mrs. L. Barrie Hunt.

INDIANA: *Hanover,* Dan Webster, Juanita Webster; *Notre Dame,* Doris Watt.

KANSAS: *Manhattan,* Greg Farley, John Zimmerman.

MAINE: *Buckfield,* Patricia Ledlie.

MARYLAND: *Aberdeen,* Barbara Bilsborough; *Annapolis,* Mark Hoffman; *Laurel,* Deanna Dawson, Sam Droege, Kathleen Klimkiewicz, John Sauer, Jeffrey Spendelow; *Towson,* Gladys Cole.

MASSACHUSETTS: *Boston,* David Morimoto, Sandra Morimoto.

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MISSOURI: *Cape Girardeau,* Dick Stiehl, Bill Whitmar.

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NEW JERSEY: *Cedar Grove,* Chris Rose, Ruth Rose; *Edison,* Robert Colburn; *Hopewell,* Hannah Suthers; *Howell,* Allen Lubchansky; *Mendham,* Susannah Graedel, Laura Graedel; *Ramsey,* Steve Rashkin; *Trenton,* Mary Doscher; *Warren,* Jay Holovacs, A. Rashkin.

NEW YORK: *Albany,* Scott Crocoll; *Allegany,* Stephen Eaton, Betty Eaton; *Apalachin,* Glenys Curran; *Binghamton,* Barbara Thomas; *Brooktondale,* Karen Allaben-Confer; *Camillus,*

Richard Roberts; *Candor,* Robert Pantle, Rita Pantle; *Delmar,* Karl Parker, Kathryn Schneider, Bryan Swift; *Ellenville,* Valerie Freer; *Ithaca,* Eric Bollinger, Cindy Braun, Greg Butcher, John Confer, Todd R. Engstrom, Christine Haselbach, Robb Reavill, Charles Smith, Scott Sutcliffe, Charles Walcott; *Lansing,* Helen Lapham; *Limestone,* Regina Vanscoy; *Middleport,* Thomas Klonowski; *Newark Valley,* Judith Bell, Lois Bingley; *New Rochelle,* Anna E. Ross; *New York City,* Dean Amadon, Tavvy Amadon, Susan Drennan, Jennifer Horne, Tony Leukering, Lester Short; *Oyster Bay,* William Kolodnicki; *Phoenix,* Cathy Slack, Roy Slack; *Purchase,* James Utter; *Schenectedy,* Robert Yunik; *Staten Island,* Albert Burchsted, Denelle Burchsted; *Syracuse,* Paul DeBenedictis, Margaret Rusk, Sarah Wiles-Ehmann; *Utica,* Kenneth Karwowski, Judith McIntyre, J. Patrick McIntyre; *Vestal,* Sadie Dorber; *Voorheesville,* George Clark.

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Ohio: *Bowling Green,* Ray Chandler; *Columbus*; Brad Andres, Abbot Gaunt, Sandra Gaunt, John Smallwood, Mary Anne Smallwood, Beatriz Torres, Thomas Waite, Mark Woodrey; *Gambier,* Jeanette Burns, Robert Burns; *Kent,* Ralph W. Dexter; *Lakewood,* Nancy Klamm, William Klamm.

Pennsylvania: *Allentown,* Daniel Klem; *Berwick,* Douglas Gross; *Bloomsbury,* Robert Sager; *Bryn Athyn,* Emily Smith, Gale Smith; *Clarksville,* Ralph Bell; *Hatfield,* Harry Mankonen; *Indiana,* Pat Merritt, Robert Merritt; *Kempton,* Stanley Senner; *Pittsburgh,* Kenneth Parkes, D. Scott Wood; *Rector,* Robert Leberman, Robert Mulvihill.

South Carolina: *Rock Hill,* Keith Bildstein, Dale Gawlik.

South Dakota: *Vermillion,* Byron Harrell.

Tennessee: *Knoxville,* Beth Lacy; *Maryville,* Ralph Zaenglein.

Texas: *Nacogdoches,* Richard Conner.

Vermont: *Fairfax,* Patricia Taber; *Northfield,* William Barnard; *Woodstock,* Walter Ellison, Sarah Laughlin, Nancy Martin.

Virginia: *Charlottesville,* Mary Clench; *Richmond,* Charles Blem, Leann Blem; *Suffolk,* Don Schwab; *Williamsburg,* Bryan D. Watts.

West Virginia: *Morgantown,* George Hall; *Ona,* Leon Wilson.

Wisconsin: *Madison,* Margaret Brittingham.

Ontario: *Toronto,* John Barlow, W. Henry Knight, Margaret May.

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By Kathy G. Beal

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